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# THE MAMMALIAN FAUNA OF THE WHITE RIVER OLIGOCENE

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## PART III. LAGOMORPHA

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# THE MAMMALIAN FAUNA OF THE WHITE RIVER OLIGOCENE

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## PART III. LAGOMORPHA

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When Professor Scott first gave me the opportunity to study the White River rodents and lagomorphs for this volume, it was with considerable trepidation and only at his insistence that I had the temerity to undertake this study of the rabbits. From my very slight acquaintance with the order, I had acquired the opinion, rather generally held, I believe, that all rabbits look alike and are nothing but mere rabbits. I had expected to base this report very largely on the works of the two men who have done most of the recent work on the earlier North American lagomorphs—Burke and Dice—and to confine myself as largely as possible to quotations from their works, with selected extracts from other authors, held together by a framework of my own authorship. At that time I knew nothing about the lagomorphs and hoped to be allowed to continue in equal ignorance. Circumstances, however, have forced me to acquire some first hand information on the subject, and as a result I have had an opportunity to develop a few opinions of my own about lagomorph evolutionary trends and relationships, although I have had practically no background of study of the order. Among the causes leading to the expansion of my program for this paper was the fact that very early in this study I had the good fortune to encounter, in my personal collections from Pipestone Springs, a considerable number of rabbit dentitions with unerupted and unworn cheek teeth, which aroused my interest in the attempt to work out cusp homologies in lagomorph cheek teeth. Further search has revealed an amazing number of such specimens in various collections and from various horizons, making it possible to work out in detail certain of the evolutionary trends within the order. Professor Case very kindly lent me the University of Michigan skeleton of *Palaeolagus*, the only White River rabbit skeleton with which I am familiar. As Dice (1933) in his description of this specimen had confined himself to a few of the more important bones, and had touched only very briefly on these, it was apparent that additional information could be made available by a further and more detailed study of this specimen. By this time it was obvious that this study was getting far from my original intentions, and that it would be necessary for me to make a very thorough study of the White River lagomorphs. The work has grown to such proportions that I believe it best to present most of the material as my own, merely attempting to indicate, wherever possible, the extent of my agreement or disagreement with previous students of the group. Very few of the points that I have raised in this paper are original with me. Although I have tried to give credit where it is due, I should like to take this opportunity to express my gratitude to those authors from whose works I have drawn most heavily, particularly Burke, Cope, Dice, Ehik and Troxell, to mention only a few. Although I have been two years working on the White River

lagomorphs, it would have been utterly impossible for me to have reached any end to the work were it not for the previous studies by Burke and Dice. The specimens on which this study is based are primarily either from my own collection or from that of the American Museum. For permission to study these last, I am deeply indebted to Dr. Walter Granger. The *Palaeolagus* skeleton was lent me through the kindness of Professor E. C. Case. A few specimens were lent me by Mr. Paul McGrew of the Field Museum, and others have been lent me from other institutions. The plates and text figure 78*a* are from drawings by Mr. Bruce Horsfall. For the text figures, I must assume full responsibility myself.

## Order LAGOMORPHA Gidley 1912

### (Suborder **LAGOMORPHA** Brandt 1859)

The lagomorphs are an order of gliriform mammals with the dental formula I 2/1 C 0/0 P 3/2 M 3/3 to 2/2. The teeth are extremely hypsodont in the earliest known forms, though the upper teeth possess only a unilateral hypsodonty, and become ever-growing in the later ones. The locomotion is quadrupedal, ranging from scampering to saltatorial. All forms are restricted to the surface of the earth. The tibia and fibula are fused in all known genera. The fibula articulates with the calcaneum. In all known forms, the portion of the maxilla on the sides of the snout is perforated either by a single large fenestra or is broken up into a lacework of bone surrounding unnumbered small openings. The jaw muscles are much weaker than in the rodents, the masseter being relatively weak and simple, with practically no trace of the division into several portions which characterizes the rodents, and the temporalis being extremely weak. The lower jaw is limited to vertical or transverse movements as opposed to the antero-posterior or diagonal ones present in the rodents. The condyle of the mandible articulates behind the glenoid fossa. The upper cheek teeth are wider than the lowers, and the upper tooth rows are further apart than the lower ones. These characters are both contrasts to the conditions in the rodents, the lagomorphs appearing to be the more primitive in these respects. The cheek teeth of the lagomorphs are in the plane of the ascending ramus, and the angle is always simple, never highly folded as is frequently the case among the rodents. There are many fundamental differences between the two orders in the soft anatomy and in the embryology, which will not be discussed here.

The Lagomorpha are a group of considerable complexity, although until very recent years it has generally been assumed that their evolutionary picture was one of the simplest of any group of mammals. With that initial assumption, it was only natural that very little work should have been done on this group, since it was thought that the main evolutionary outline was already known, and that further work would only fill in some of the minor details. It was believed that each of the two families comprising the order, the Leporidae and the Ochotonidae, were monophyletic and that the former, at least, was directly derivable from *Palaeolagus*, which was thought to be the only White River representative of the order. Recent work, however, primarily by Dice, Gazin and Burke, has shown that there were a large number of unexplored and little known phyla of lagomorphs. The ochotonids have been traced back into the Oligocene of Europe. They are entirely unknown, however, from the earlier Tertiary of North America or Asia, since Burke has shown that *Desmatolagus* was a leporid (Burke, 1936, pp. 149–153). It is undoubtedly

true that the leporids and ochotonids must have had a common ancestor, and that the Oligocene forms are nearer to that ancestor than are the Recent types, but there is no possibility of connecting the two families through any of the White River genera, or even through the Uinta *Mytonolagus*, since these are all definitely leporids. Concerning this matter, Burke states that "There can be no doubt that *Mytonolagus* is near the stem stock from which both the *Leporidae* and *Ochotonidae* diverged, and in many respects can be taken as structurally ancestral to both families. However, a great deal of comparative study is required before any confident statements can be made as to the interrelationships of the earlier genera which have been referred to the *Leporidae* and to the *Ochotonidae*" (Burke, 1934, p. 415). Schreuder paraphrases this slightly, as follows: "*Mytonolagus* is slightly more primitive than *Palaeolagus*, and largely resembles *Desmatolagus* from the Oligocene of Mongolia. However, the former certainly belongs to the Leporidae; the Asiatic genus may be an Ochotonid, although $M\overline{3}$ is present in a rudimentary state. At any rate both are near the stem stock from which the Leporidae as well as the Ochotonidae diverged" (Schreuder, 1936, p. 235). From what information is now available, I do not believe that either of these genera could be ancestral to the ochotonids. Consequently, it would appear that the common ancestor of the two families must have lived at least as early as Bridger time. In the following pages *Ochotona* has been used for comparison with White River forms, not with the idea of indicating relationships, but because it represents a particular stage in lagomorph skeletal evolution and because it is hoped in this manner to arrive at a better understanding as to which characters of the fossils are those of the primitive lagomorph stock, which are those of primitive leporids, and which indicate specializations of the Oligocene forms in directions all their own.

A very natural tendency on the part of early taxonomists was to unite into a single order all the mammals that were primarily gnawers. Subsequent work has shown that a number of these forms could have no real relationship with the true rodents, the resemblances being convergences from entirely different original sources, brought about because these animals had developed the same sort of use for their incisors as had the rodents. No serious student would now question the statement that the Multituberculates, *Phascolomys*, *Chiromys* and its relatives, the Taeniodonts, and the Typotheres have no real relationship to the rodents. For the last seventy-five years at least, it has been realized that there is a very marked separation between the Duplicidentates and the Simplicidentates, Schlosser (1881, p. 131), for example, saying "Die Abzweigung der *Lagomorpha* von den *Marsupialiern* dürfte wohl erst in späterer Zeit erfolgt sein, als die übrigen Nager." Most taxonomists, not familiar at first hand with these groups, even up to recent years, have confined themselves to separating the rodents into two distinct suborders, the Duplicidentates and the Simplicidentates (see, for example, Simpson, 1933). Specialists on these groups, however, came some time ago to the conclusion that the Duplicidentates were another group whose union with the rodents was unnatural. Gidley (1909) first, I believe, proposed their separation, and named the new order containing the rabbits and coneys the Lagomorphs, using Brandt's subordinal name, although Tullberg had clearly recognized the wide separation of the Simplicidentates and the Duplicidentates a number of years earlier, as shown by the following quotations. "Während die Abweichungen sehr gross und wichtig sind, kann man nämlich sagen, dass die Übereinstimmung zwischen ihnen, ausgenommen gewisse Ähnlichkeiten im Zahnsysteme, sich auf eine Anzahl Charaktere beschränkt, welche

sie mit mehreren anderen Ordnungen der Säugetiere gemein haben. Am meisten beachtet von jenen Ähnlichkeiten im Zahnsystems ist die starke Entwicklung der beiden mittleren Vorderzähne und die bei beiden Gruppen im Zusammenhang damit auftretende Reduktion einiger Vorderzähne, des Eckzahns und der vordersten Backzähne. Diesen Übereinstimmungen darf indes kein besonders grosses Gewicht beigelegt werden, teils weil die Vorderzähne sich bei den fraglichen Gruppen recht abweichend entwickelt haben, indem die *Duplicidentaten* im Oberkiefer vier Vorderzähne beibehalten haben, und auch die beiden hinteren thatsächlich fungieren, teils ferner, weil eine ähnliche Zahnreduktion auch bei anderen Gruppen von Säugetiere auftritt, welche indes keine sonderliche verwandtschaftliche Beziehungen zu den *Glires* aufzuweisen haben" (Tullberg, 1899, pp. 336–337). He then proceeds to state that the gliriform development of the incisors has proceeded as far in Hyracoids and Typotheres as in the lagomorphs, and as far in *Chiromys* and *Phascolomys* as in the rodents. After citing similarities in cheek tooth structure between the two groups, he proceeds to state: "Sehr grosses Gewicht ist allerdings auf diese Übereinstimmung nicht zu legen, da die Art und Weise des Kauens bei den *Duplicidentaten* und den *Simplicidentaten* so verschieden ist, und es anzunehmen sein dürfte, . . . dass die noch aussen gehende Richtung der oberen Backzähne bei Diesen von ganz anderen Ursachen abhängt, als bei Jenen" (op. cit., p. 337). After citing embryological similarities, he continues "so finde ich es am angemessensten, wenigstens bis aufs weitere die *Duplicidentaten* und die *Simplicidentaten* innerhalb der Ordnung *Glires* beizubehalten. Ein Grund, diese beiden Gruppen nicht weiter auseinander zu halten, ist auch, dass es unter den Säugetieren keine andere Gruppe giebt, mit der die eine oder die andere dieser beiden Gruppen als enger verwandt betrachtet werden kann" (op. cit., pp. 337–338). This last statement, of course, is equally true today, but it does not appear to be a valid reason for uniting the two groups in view of all the evidence of their wide separation from each other.

"Wenn man nun demnach annimmt, dass die *Duplicidentaten* und die *Simplicidentaten* einer Ordnung angehören, muss man natürlich auch annehmen, dass beide Gruppen einer gemeinsamen Stammesform entstammen, welche bereits vor ihrer Differenzierung sich von übrigen *Placentalien* getrennt hatte. Damit sei jedoch keineswegs behauptet, dass diese Form sich bereits zum Nager entwickelt habe. Es kommt mir viel warscheinlicher vor, dass die beiden fraglichen Gruppen, bereits ehe sie zu eigentlichen Nagetieren wurden, aus anderen Ursachen zu differenzieren begonnen hätte, und dass erst späterhin jede Gruppe sich zu Nagern ausbildete" (op. cit., p. 338). This opinion is not so very far in fundamentals from what seems to me to be the most reasonable position at the present time. There seems to me to be no doubt that the rodents and lagomorphs have been separate groups at least as long as they have been rodents and lagomorphs, exactly the position maintained by Tullberg in the above quotation. If this be accepted as true, most modern taxonomists would agree that they should be considered distinct orders, though the possibility should be kept in mind that they may have sprung from a common stock after that common stock had separated from the primitive insectivores. If this should eventually turn out to be what actually occurred, the term "Glires" could well be used in its original Linnaean sense, for the rodents, lagomorphs, and their common ancestors. At the present time, however, there is no evidence whatsoever that the two orders are specially related, except for their parallelism, which, following the principle that the closer the parallelism, the closer the relationship, would indicate that these two orders are closer to each other than either is to any other known group of mammals.

For those who have worked with the rodents or lagomorphs, no explanation of the necessity for their separation is needed. For the sake, however, of those not familiar at first hand with the evidence, a brief summary of some of the more striking differences is presented here.

In the earliest known rodents (from the lowest Eocene and uppermost Paleocene), the dental formula is I 1/1 C 0/0 P 2/1 M 3/3, whereas in the lagomorphs the formula is I 2/1 C 0/0 P 3/2 M 3/3 to 2/2, which shows that the lagomorphs could not have been derived from any known rodent without a reversal of evolution entirely without parallel. In fact, it is unquestionably true that the Eocene and Oligocene rabbits differed more from the contemporary rodents than do the modern rabbits from the modern rodents. This strongly suggests that all the similarities between the two orders are due to convergence. The pattern of the upper molars of the lagomorphs will be discussed in detail below, but it may be pointed out here that it has no close similarity to that of any of the rodents. The pattern of the lower teeth is equally divergent. Most of the similarities are merely indicative of tritubercular ancestry. The others are resemblances between the *worn* teeth of lagomorphs and the equally worn teeth of some of the more specialized rodents. The articulation of the fibula with the calcaneum, present to as marked a degree in the Lower Oligocene as at present, is a striking difference from the rodents, and the details of the pes are quite distinct in the two orders. In the lagomorphs, the whole posterior portion of the mandible is in the plane of the alveoli, showing none of the folding or bending seen in the rodents. Finally, even though the tempo of evolution of the rodents is relatively slow—often being far slower than is generally thought—that of the rabbits is very much slower, approaching in its rate that of the opossum. Hence, although the rodents, if their known rate of evolution in the Tertiary were carried back of the Eocene, would be very close to the placental stock in the lower Paleocene or uppermost Cretaceous, a similar extrapolation of lagomorph evolutionary rates would show them still to be typical lagomorphs well back into the Cretaceous. Perhaps this point will not carry great weight with those who are not familiar at first hand with the two groups, but to those who have studied these animals, I believe that this difference will seem of significance. The mere fact that a particular evolutionary rate has been followed by the rodents and lagomorphs since they first appear does not, of course, establish that the same rate was followed at previous periods, but until they can be shown to have evolved at a different rate, the safest assumption is that the rate was relatively constant.

### Family Leporidae Gray 1821

The leporids are the larger and more progressive lagomorphs. All the saltatorial forms belong to this family. The maxilla is broken into a lacework of bone instead of there being a single large vacuity as in the ochotonids. The lateral margin of the nasal extends further caudad than any of the rest of the bone, and ends in a sharp point, whereas in the ochotonids this end of the bone is gently rounded and its most posterior point is in the center of the bone. There is a supraorbital process of the frontal. Since this is absent even in the Miocene ochotonids (Schlosser, 1884, Fig. 1), it is almost certain that this is a specialization of the leporids, and that it was absent in the ancestral lagomorphs. The snout tapers anteriorly, instead of its sides being parallel as in the ochotonids. There is a circular pit on the lateral surface of the zygoma. The zygoma is a vertically expanded

plate, instead of being a slender rod as in ochotonids. The talonids are attached to the trigonids by a broad peduncle, extending across all, or nearly all, of the width of the tooth. The dental formula is always I 2/1 C 0/0 P 3/2 M 3/3. In distribution this family is nearly world wide, occurring naturally in all the continents except Australia. The geologic distribution is from Upper Eocene to the present.

### Subfamily Palaeolaginae Dice 1929

Dice defined the subfamily as follows: "Main external reëntrant angle of the enamel on the face of $P\overline{3}$ not extending beyond the middle, and usually meeting a strong internal reëntrant angle. The enamel pattern therefore forms an hour-glass-shaped figure, and the tooth is formed of two vertical columns of dentine, standing one in front of the other" (Dice, 1929, pp. 340–341). As will be shown below, this diagnosis characterizes the teeth of *Palaeolagus* during most of the life time of the individual. In old age, however, the teeth become those of a member of the Archaeolaginae. It is possible that these two subfamilies are really distinct, but it is virtually impossible to draw any line between the two at present. *Megalagus*, for example, is a palaeolagine for a third of its life and an archaeolagine for two thirds. As far as the fossils are concerned, these two groups are very closely related. I believe that the Palaeolaginae could better be defined merely as "leporids in which $P\overline{3}$ is divided into two lobes, the anterior of which is simple and without accessory invaginations." Probably careful study of the unworn cheek teeth of Miocene and later leporids would furnish additional characters, possibly of subfamily significance, which might warrant the retention of the Archaeolaginae. It is also quite probable that important characters would be observed by a careful comparison of the skulls and skeletons of Oligocene and Miocene leporids. For the time being, however, I think it would be the best exposition of present day information to assume that the Leporidae are divisible into Leporinae and Palaeolaginae (= Palaeolaginae + Archaeolaginae in the sense used by Dice in 1929). Dice himself appears to be less certain of the validity of the Archaeolaginae, stating (1932, p. 381) that in young individuals of *Hypolagus browni* "the enamel would . . . have had the pattern characteristic of *Palaeolagus* and other genera of the subfamily Palaeolaginae. This may indicate that the genera *Hypolagus* and *Archaeolagus*, which I have placed in a separate subfamily Archaeolaginae, originated from the Palaeolaginae." Kormos (1934) and Schreuder (1936) have also reached the conclusion that the Archaeolaginae were not validly separable from the Palaeolaginae. Burke, unfortunately, has never expressed himself on paper about subfamily relationships.

Dice's subdivision of the Leporidae was based primarily on the characters of $P\overline{3}$. This has proved a useful and convenient method of separating the subfamilies. The danger of using a single character is shown by the example of Walker (1931*a* and 1931*b*), who erected two additional subfamilies, one, the Protolaginae, being based on immature specimens of *Palaeolagus haydeni*. The typical Oligocene leporids are certainly a closely related stock. Their separation or unification will depend largely on whether one believes in a horizontal or a vertical classification, and upon what one believes the phylogeny of the leporids to have been. *Megalagus* is probably at least structurally descended from *Mytonolagus*, from which *Palaeolagus* probably is not descended, and therefore the two genera cannot have had a common ancestor later than the earliest Uinta. In spite of this long time separation, *Megalagus* is undoubtedly morphologically close to *Palaeolagus*, due, of

course, to the slow rate of lagomorph evolution. These Oligocene rabbits vary in the size of the internal fold of $P\bar{3}$ from typical *Palaeolagus* with the inner fold almost equal in length to the outer, through senescent individuals of the same genus, in which the inner fold has been destroyed by wear, to typical *Megalagus*, in which the inner fold is preserved only a very short time before it is worn away. This shows the impossibility of drawing hard and fast lines on the basis of the characters of this tooth. In the Palaeolaginae the hypostria is shallow, and does not persist throughout life. In all the other leporids, the hypostria remains as a deep groove, persisting throughout nearly all, if not all, of the individual's life. At the same time, the other elements of the crown pattern are much more persistent in the Palaeolaginae than in the later forms. This, of course, is not a sharply differentiating character, but merely represents the interaction of two plastic parts of the animal, one of which grows at the expense of the other. When the hypostria develops to such a point that it lasts longer than the rest of the crown pattern, the animals have ceased to be palaeolagines and have become archaeolagines. This distinction, of course, is entirely arbitrary, but it is the only one that at present seems to permit the separation of the palaeolaginae into two subfamilies.

At the present time, it would be extremely rash to assume that the palaeolagines are directly ancestral to the leporines, although they are certainly close to the ancestral stock. Neither has it been established that the later members of the subfamily have been descended from the known Oligocene forms. Although there are several living genera of palaeolagines, they have been distinctly less successful than the members of the Leporinae. All the modern palaeolagines are limited to restricted areas in rather out of the way parts of the earth, where they would have been but little affected by Tertiary migrations and would not have been brought into contact with the higher leporids. Their present distribution is distinctly peripheral, in accordance with Matthew's ideas (Matthew, 1915). The Palaeolaginae are represented in the White River by *Palaeolagus*, *Megalagus* and *Desmalolagus*, discussed below in that order.

### **Palaeolagus** Leidy 1856

*Palaeolagus* Leidy, Proc. Acad. Nat. Sci. Phila., Vol. 8, 1856.
*Tricium* Cope 1873*c*.
*Protolagus* Walker 1931*b*.

(Plates XXXV–XXXVI)

Genotype: *Palaeolagus haydeni*, Leidy 1856.

*Palaeolagus* is the only really abundant American Oligocene rabbit. It is represented by the remains of thousands of individuals in every collection from the White River Oligocene, and is unquestionably, I believe, the most abundant genus in the White River. Cope pointed out this fact long ago (1884, p. 874). In a small collection that I made in 1935 were the remains of several hundred members of this genus, a couple of dozen specimens of *Megalagus*, and two or three of *Desmatolagus*. Aside from its overwhelmingly greater abundance than any of the contemporary rabbits, there are certain clear cut characters by which this form may be recognized. In size it is the smallest of all the Oligocene leporids, excepting only *Desmatolagus gazini*. The tooth pattern is very distinct from that of *Desmatolagus*, the external crescent of the upper teeth being united with the other buccal por-

tions, so that a worn tooth develops a crescentic enamel lake between the external crescent and the lingual portions of the tooth. The internal fold of these teeth is more persistent than in *Megalagus* or *Desmatolagus*. The teeth are very much more hypsodont than in the other genera, the buccal roots never being present. As a result, the buccal portions of the tooth are not weakened by the loss of the roots as is the case in the other genera. Cement is present very profusely over the crowns of erupted teeth. $P\bar{3}$ has strong internal and external folds, the former persisting much longer during the life of the individual than in the other forms. Certainly in the Oligocene, since the development of this fold is to a large extent an age character, it should not be advisable to separate subfamilies of leporids until more information is available as to the skeletons of *Megalagus* and *Desmatolagus*. When $P\bar{3}$ is unworn, it shows the external fold in the talonid (the metastriid) which Walker (1931*b*) used as the characteristic feature of his genus *Protolagus*. Although I have not seen the diplotype of *Protolagus*, from Walker's description there does not appear to be any doubt that this was merely a juvenile *Palaeolagus haydeni*. Fortunately, Dice and Dice (1935) had an opportunity to study Walker's type, and reached the conclusion that this was definitely a juvenile *P. haydeni*. Their illustration of the teeth removes all possibility of doubting their conclusion. The accompanying illustrations of this tooth (Figs. 86 to 91) show the changes in pattern with advancing age, and leave no possibility for questioning the fact that this form is synonymous with *P. haydeni*. *Tricium* Cope is unquestionably based on the deciduous lower molars of *Palaeolagus haydeni*, as Cope himself recognized.

The upper cheek teeth of *Palaeolagus* are characterized by an extremely shallow internal fold, which changes into a small groove after relatively little wear. A prominent feature of the crown pattern is the central V, which generally persists during most of the animal's life as a lake separate from the internal fold. In this it differs from *Megalagus*, *Desmatolagus* (Matthew and Granger, 1923, Fig. 10a) and *Titanomys* (Ehik, 1926, Fig. 1). In the discussion of the teeth of the White River lagomorphs, I have used the tritubercular nomenclature, without any present desire to suggest the homologies of the parts. A later section (pp. 351–356) will deal with certain possible interpretations of the fundamental leporid dental pattern, in which the usage adopted will be explained and perhaps justified.

The skull is essentially similar to that of modern rabbits in its general outlines. Most of the characteristic rabbit features are present, though developed to a much smaller degree than in Recent forms, or even than in the John Day forms. The post-orbital processes are smaller, the palate less reduced, the fenestrations of the snout less accentuated, and the bending of the face on the basicranial axis less advanced, than in any later leporids. The skeleton appears to be that of a scampering form, more like *Ochotona* in its habits than like even the cottontails.

*Range:* Entire Oligocene (Pipestone Springs to Leptauchenia Beds) of the Great Plains province of the United States; Lower Oligocene of Saskatchewan; and possibly Lower Miocene of Wyoming and Texas.

"The size of the skull is very small for a rabbit . . . , being smaller than that of the sage rabbit *Sylvilagus* (*Brachylagus*) *idahoensis*, which is probably the smallest living member of the Leporidae. The fossil skull also is considerably more flattened dorso-ventrally than is the skull of any living kind of rabbit or hare. Further, it is much less arched than the skull of any other genus of the Leporidae. The angle between the planes of the basioccipital and the palate is only 16.5 degrees" (Dice, 1933, pp. 301–302). These differences

involve a number of clearly marked evolutionary modifications, in all of which the Leporidae have diverged from the Ochotonidae. The brain-case of modern leporids is much more inflated than is that of *Palaeolagus*, which accounts for a considerable part of the difference in the arching of the skull. This arching is present only to a slight degree in the pika. At the same time, there has been a marked downward bending of the face on the basicranial axis, which has not taken place in *Ochotona*. The marked extent to which this bending has occurred in the Recent leporids is shown by an infant *Sylvilagus* in the author's collection, in which the angle between the basicranial and basifacial axes is about forty degrees, as in the adult of the same form. This change is undoubtedly correlated with the position in which the animal carried its head. It would seem that the head was carried lower than in Recent forms, and more nearly as a continuation of the line of the vertebral column, thus approaching more closely to the position in which the head is carried by scampering forms, such as the rats or ground squirrels. In general, the proportions of the skull are so similar to those of the skull of *Ochotona* that it seems quite probable that the method of locomotion was very similar in the two forms. The orbit is directed laterad as in Recent leporids, rather than upward as in the pika. It is much smaller than in Recent lagomorphs, being 24% of the total length of the skull in *Palaeolagus*, as against 26% in *Ochotona* and 28% in *Lepus* and *Sylvilagus*. This suggests the possibility that *Palaeolagus* was more diurnal in its habits than are the Recent lagomorphs.

In dorsal view, there are quite a number of differences between *Lepus* and *Sylvilagus* on the one hand, and *Palaeolagus* on the other. The skull is much more elongate in the first two than in the last. This is particularly true of the snout, though it characterizes the entire skull. The zygomata are appressed much more toward the middle line, and are much more nearly parallel to the long axis of the skull in the fossil than in the Recent leporids, or than in *Ochotona*.

The *nasals* extend slightly anterad of the incisors, in striking contrast to adult specimens of *Lepus* and *Sylvilagus*, in which the incisors extend well forward of the nasals. This is another character in which the fossil agrees with the pika. The lateral margins of the nasals are nearly parallel, and the postero-lateral tips extend farthest caudad of any part of the bones, as in the modern leporids. This is entirely different from the situation in *Ochotona*, where the posterior ends of the nasals are gently rounded, and the middle portion of each bone reaches slightly farther caudad than any of the other portions. The median notch is very slight in the pika. The lateral margins of the nasals are nearly parallel, but diverge slightly near the posterior end, as in the modern leporids. Just the opposite is the case in the pika, where the divergence is anterad. There is not, however, any trace of the elongate median process of the frontals which separates the nasals in *Sylvilagus*, and, to a lesser extent, in *Lepus*, but merely a broad embayment. Anteriorly, the nasals are slightly arched, as in the modern forms. No trace has been seen in any *Palaeolagus* of the extensive group of nutritive foramina slightly anterad of the middle of the nasals in *Sylvilagus*, and developed to a lesser extent in *Lepus*. This is obviously a primitive character in the fossil, and one in which it agrees with *Ochotona*. The posterior divergence of the nasals would appear to be a heritage character of the leporids, whereas the forward extension of the incisors in Recent leporids would appear to be a habitus character, divergent from the primitive lagomorphine heritages, suggestive of a possible increase in fossorial habitus, even though none of the leporids are truly fossorial.

The *frontals*, in their general outline, are rather similar to those of other leporids, and quite different from those of the ochotonids. They possess supra-orbital processes which appear to be ancestral to those of the Recent leporids. As a result, the inter-orbital part of the frontals has the greatest diameter of any part of the bones, instead of the least as in the pika. The process arises in approximately the same position as in *Lepus* and *Sylvilagus*, but is very much smaller, being directed posterad and laterad in a single wing, instead of having the posterior and the anterior wings of the Recent forms. The process does not extend as far posterad as in the modern forms, leaving a wide opening between its extremity and the zygomatic process of the squamosal, quite different from the situation in *Lepus* and *Sylvilagus*. In the fossil, the process is united to the rest of the frontal by a broad base, instead of by the narrow one as in *Lepus*. In this it resembles *Sylvilagus*. The process arises in *Palaeolagus* from the frontal just behind the posterior end of the nasals, instead of some distance from this point, as in the Recent genera. There does not seem to have been any of the antero-posterior arching of the process which is so noticeable in the living genera. According to Dice, "This process is somewhat imperfect in all the specimens, but it probably resembled that of *Romerolagus*, a member of the same subfamily, Palaeolaginae, living today on an isolated mountain mass in Mexico" (Dice, 1933, p. 302). There is a slight depression between the main part of the frontal and the process, though it is not as marked as in *Sylvilagus*. This groove does not appear to occur in *Lepus*. Small nutritive foramina appear here in *Palaeolagus*, as in *Sylvilagus*. The frontals extend forward, ending in a blunt process between the nasals, which is not, however, as well marked as in the other leporids. *Palaeolagus* also possesses a sharp lateral process between the premaxillary and the maxillary, which is present in both Recent leporids and in the pika, and which therefore would seem to have been a character of the ancestral lagomorphs, as opposed to the supra-orbital process, which is merely a leporid character. The frontal narrows just behind the supra-orbital process, resembling that of *Lepus* in this respect, and differing noticeably from that of *Sylvilagus*. Posteriorly, the frontal does not join the squamosal on the dorsum of the skull, as it does in the Recent leporids, thus representing a more primitive condition. The reduced size of the frontals and the forward growth of the parietals in the pika is an aberrant development of the ochotonids, but seems to trace back to a condition very much more primitive than anything seen in *Palaeolagus*. The posterior end of the frontal crosses the dorsum of the skull in an almost straight line, instead of having the irregular suture seen in the Recent leporids. It is more like *Ochotona* in this respect. The posterior margin of the frontal has about the same relationship to the glenoid fossa as in living lagomorphs, which suggests that a large part of the arching of the skull in the latter forms has been due to a forward growth of the cerebrum during rabbit evolution. There are none of the nutritive foramina in *Palaeolagus* which appear widely scattered over the dorsum of this bone in *Sylvilagus*. The frontal overhangs the orbit, forming a roof over a considerable portion of that cavity. It also forms the median wall of the dorsal half of the orbit, articulating with the lachrymal anteriorly and with the orbitosphenoid and parietal posteriorly, as in the modern rabbits. There is a small ethmoid foramen just above the orbitosphenoid-frontal suture. Anteriorly, the frontal extends ventrad in a marked process between the lachrymal and the orbitosphenoid, as in *Sylvilagus*, but differing in this respect from *Lepus*, where this process is absent, its place being taken by an ascending process of the maxillary.

The *lachrymal* was very loosely attached in *Palaeolagus*, as it is in Recent genera, and is

usually represented only by a large vacuity, as is likewise the case with specimens of modern genera picked up on the plains. It is preserved, however, in A.M.N.H. No. 5738. The bone is quadrate, and approximately the same relative size as in Recent leporids. Its ventral margin is hidden by the upgrowth of the maxillary around the bases of the cheek teeth, though this process has not advanced to the same stage as in the living forms. The lachrymal foramen seems to have been slightly larger in the fossil than in the Recent forms. In none of the lagomorphs does this bone appear to have extended onto the face to the slightest degree.

The *parietal* plays a larger part in the formation of the roof of the skull in *Palaeolagus* than it does in other members of the family. The bone is nearly flat, as in *Ochotona*, instead of being greatly arched by the upgrowth of the cerebrum, as in *Lepus* and *Sylvilagus*. Laterally, it extends farther forward, reaching the temporal fossa just anterad of the glenoid fossa, whereas in Recent leporids, the backward growth of the frontal and the forward growth of the squamosal have separated the parietal from the temporal fossa. In *Palaeolagus*, the parietal extends far enough into the temporal fossa to come into contact with the alisphenoid. For two thirds of its length, the parietal articulates with the squamosal in about the same manner as in the modern forms. Posterior to this point, however, the bone continues almost straight back in *Palaeolagus*, articulating with the supraoccipital laterad of the end of the interparietal. This results in a sharply angulate postero-external corner of the bone in the fossil, in sharp contrast to the rounded outline seen in Recent lagomorphs, due to the mesiad curve of the lateral margins of the bone. There are no nutritive foramina in the parietal of any specimen of *Palaeolagus* that I have seen, differing sharply in this respect from *Sylvilagus*, and, to a lesser extent, from *Lepus*. The parietal extends practically to the posterior end of the skull in *Palaeolagus*, in the normal mammalian manner, the invasion of the dorsal surface by the supraoccipital being a later development of rabbit evolution. The entire absence of this in *Ochotona* shows it to be a leporid specialization, perhaps brought about by a spread of the neck muscles onto the dorsum of the skull, carrying the supraoccipital with them. This strengthening of the muscles undoubtedly occurred as a jumping adaptation.

The *interparietal* is larger than in Recent forms, and fuses with the parietals later in life. The bone has a long, sharp anterior process, which is entirely absent in the modern forms, where its anterior end is more rounded. The nutritive foramina seen in this bone in modern leporids do not appear in the fossil. In the living forms, due to the rounding of the lateral corner of the parietal, the interparietal extends much farther caudad than do the parietals. This is not the case in *Palaeolagus*, where the postero-external processes of the parietals form a straight transverse line with the posterior margin of the interparietal. In *Ochotona*, the bone appears to be very minute, and to have a shape quite different from that in the leporids.

The *supraoccipital* extends for only a short distance onto the top of the skull, as in *Ochotona* and mammals in general, in sharp contrast to the other leporids. In these last forms there is a quadrate median table formed by the supraoccipital, no trace of which exists in *Palaeolagus*. In the Recent forms, the cerebellum is covered by the supraoccipital, whereas in *Palaeolagus* it was covered by the parietals.

The differences in the lateral view between the fossil and the Recent genera are due primarily to the inflation of the brain and the bulla, the bending of the facial on the basicranial axis, and the increase of fenestration in the maxilla of the Recent genera. The orbit

of the Recent forms has grown at the expense of the temporal fossa, which is nearly equal in size to the orbit in *Palaeolagus*, but which is reduced almost to non-existence in the living genera.

The *premaxillary* reaches its greatest development on the lateral aspect of the snout. In the middle of the side of the snout, there is a strong posterior process of this bone, fitting into a wide notch in the maxillary. This is absent in the modern forms, where it appears to have been shortened by differential growth of the maxillary. This is perhaps only to be expected, since the apparently progressive tendency toward the increase of these reticulations suggests that the region they occupy is one of dominant growth tendencies. The bone is proportionately much higher in *Palaeolagus*, which appears to be due merely to the growth of the notch between the nasal and the premaxillary—growth which has taken place at the expense of the latter. In the fossil, this notch reaches barely to the incisor, whereas in the Recent genera it has extended posterad of the main body of the premaxillary. If it is permissible to consider this an analogy with the proboscidea, where the reduction of bone in the narial region is associated with extreme mobility of the proboscis, it would seem possible that the development of this notch and the shortening of the nasals in the Recent leporids might be correlated with the well known ability of the rabbit to wiggle its nose. If this interpretation is correct, it thereupon follows that *Palaeolagus* must have lacked this ability, at least in the marked degree to which it is present in the living genera. Correlated with the shallowness of this notch, the incisor is proportionately much larger and extends farther dorsad, being an arc of a larger circle, in *Palaeolagus* than in *Lepus* or *Sylvilagus*. *Ochotona* is very like *Palaeolagus* in this respect. The anterior end of the premaxilla does not extend as high in the pika as in *Palaeolagus* since the nasals are somewhat more tubular and extend farther down on the side of the face in the former. This is correlated with the fact, mentioned above, that in the pika the nasals are widest at their anterior ends, in contrast to the situation in the leporids. The postero-dorsal process of the premaxillary is as long and slender as in the Recent forms, reaching as far as the level of the zygoma. In *Ochotona*, it does not extend as far posterad as this, ending well forward of the posterior end of the nasals. In the leporids, on the other hand, the premaxilla extends almost as far back as do the nasals. There are a few nutritive foramina near the dorsal part of the premaxilla, similar to those in the same position in *Lepus* and *Sylvilagus*. Ventrally, the premaxillae are similar in *Palaeolagus* to those in the Recent leporids, tapering slightly toward the anterior ends in contrast to *Ochotona*, in which the sides of the snout are parallel. *Palaeolagus* differs from all the Recent forms, however, in that the incisive foramina extend forward to, or even actually between, the posterior incisors, instead of terminating an appreciable distance behind them. This appears to be a primitive condition in the fossil, the narrowing of the snout in all the living forms having forced the two rami of the premaxillae toward each other anteriorly, thus tending to close the anterior ends of the foramina.

The dorsal part of the *maxillary* is reduced to a lacework of bone, though the reticulate area does not extend as far ventrad as the infra-orbital foramen, and is, in fact, separated from it by a well marked, though narrow, band of solid bone. In the modern leporids, of course, the reticulations extend to or below the level of the foramen, and the area of solid bone has been greatly reduced, the foramen being merely the largest of an extensive group of openings in the maxillary. In the pika, the network has been replaced by a single large fenestra, separated from the foramen by a slender rod of bone. This appears to be the

logical end stage of the process represented in the leporids. Apparently, this stage had already been attained in the Miocene, Schlosser stating that the skull of *Myolagus* was very like that of the living *Lagomys* (1884, p. 11). In *Palaeolagus*, the vacuities make up less than half of the area of that portion of the maxilla in which they occur. In the modern genera, the bone has been reduced to mere threads, and the fenestrations occupy by far the largest part of the area. This appears merely to be an exemplification of the normal procedure during fenestration, the borders of the fenestra being strengthened, and the bone removed from the central portion. In this instance, the process is complicated by the presence of a large number of coalescing fenestrae, instead of there being merely one or two dominant ones. If the development of these fenestrae is simply an economy in the deposition of bone, there is probably no functional purpose behind its progressive development. In *Palaeolagus*, the fenestrations are not as well developed in adolescent as in adult animals. This is in agreement with the condition in modern forms, Davis (1936, p. 39) saying in regard to the young of the brush rabbit that "there is no indication of rostral fenestrations which are so characteristic of older skulls." It must follow from this that the bone is first deposited and then resorbed, the reticulate pattern being the result of differential resorption. The infra-orbital foramen is lower on the face in *Palaeolagus* than in *Lepus* or *Sylvilagus*, more nearly resembling the pika in this respect. The canal runs almost horizontally from the face into the orbit, instead of being inclined postero-ventrad as in living leporids. It is proportionately larger than in the Recent genera. The anterior part of the zygomatic process is nearly vertical, and extends abruptly outward from the snout, as in living rabbits, though not to as marked a degree. This is further advanced in *Palaeolagus*, however, than in *Ochotona*. On the anterior face of the zygoma there is a circular pit, similar to that in *Lepus* and *Sylvilagus*, though nowhere near as deep. There is no trace of this in the pika. The basal portion of the cheek tooth prisms extends into the orbit, forming a large tuberosity as in the living rabbits, though it reaches barely above the level of the zygoma and does not restrict the infra-orbital canal, whereas in *Lepus* and *Sylvilagus*, the continued and accentuated hypsodonty of the cheek teeth has carried the higher part of this tuberosity, where the growing germs of the teeth are located, halfway up the orbit, greatly constricting the posterior opening of the infra-orbital canal, reducing it to a narrow fissure between the tuberosity and the rest of the maxillary as far posterad as M3, and thus past the posterior margin of the lachrymal. As in leporids in general, the bone covering this tuberosity is very thin, and frequently or even usually is fenestrated over the pulp cavities of the cheek teeth. This is especially characteristic of isolated maxillae of *Palaeolagus* bearing a single cheek tooth series. It is possible that the invasion of the orbit by the cheek teeth so reduced the vertical diameter of the orbit that it was forced to expand posteriorly, and that this is the basic cause of the increased size of the orbit in the Recent leporids as contrasted with *Palaeolagus*. This tuberosity helps to hold the lachrymal in place in cleaned skulls, particularly those of *Lepus*. There is no trace of this tuberosity in *Ochotona*, in which the basal portions of the cheek teeth pass laterad of the orbit instead of mesiad, entering the zygomatic process of the maxilla, and form a strong lateral wall to the orbit. This is another significant point of divergence between the two families, pointing to their separation before any development of hypsodonty in either group, and hence at least before the beginning of the Oligocene. On the ventral surface, the maxillary is as reduced as in the living rabbits. The palatine fenestrae end by the anterior end of P2, as in *Mytonolagus*

(Burke, 1934, Pl. L, Fig. 1), instead of at its middle as in *Sylvilagus*, or at its posterior end, as in *Lepus*. The branches of the maxillae forming the lateral borders of the fenestrae are heavier in *Palaeolagus* than in the living genera, since the posterior portion of the fenestrae has expanded in these latter forms, whereas it is of uniform width in the fossil. In *Ochotona*, the fenestrae have extended backwards to the posterior margin of P3, and have expanded into a bulbous posterior end. The maxillae are extended in sharp processes between the posterior ends of the fenestrae, as in leporids, but differing in this from the pika. From Burke's figure (op. cit., Pl. L, Fig. 1), it would appear probable that there was no trace of these median processes in *Mytonolagus*. Posteriorly, the maxilla is heavily notched by the palatine, which extends forward along the midline in a triangular process, a condition not seen in Recent rabbits, where the maxillo-palatine suture runs almost directly across the palate. *Mytonolagus* is similar in this character to *Palaeolagus*, though the tip of the process reaches to the anterior end of P4 in the Uinta form, and only to its posterior end in *Palaeolagus*. The fundamental difference between the fossil and Recent genera is that in the latter the lateral margins of the palatines have grown forward until they have attained the same level as the median tips of the bones. The maxilla is generally of approximately the same size in the Recent forms as in *Palaeolagus*, its principal reduction being due to the expansion of the palatine fenestrae. The alveolar process of the maxillary covers a broader portion of the palate than is the case in modern forms, in which it has been overlapped by the palatine almost to the alveolar borders. The zygomatic process is similar to that in living leporids, though the circular pit just above the masseteric fossa is considerably shallower in *Palaeolagus*. The fossa is not so sharply separated from the surrounding portions of the bone as is the case in modern forms, a character which merely indicates an expectable lesser development of the masseter in *Palaeolagus* than in living leporids. From Burke's description, it would appear that there is almost as much difference between the zygomata of *Mytonolagus* and *Palaeolagus* as between those of the latter and *Sylvilagus*.

The *malar* is fused with the maxillary in adult specimens, as is the case in Recent forms. In young individuals, however, even though fully grown, the suture can be seen quite clearly below the middle of the orbit. Posteriorly, the malar continues as a slender vertical plate, extending behind the glenoid fossa and below the zygomatic process of the squamosal. Although the malar does not enter into the glenoid, this posterior process would undoubtedly serve as an aid in preventing excessive lateral movement of the condyle of the lower jaw. There is no indication in any leporid that I have seen, and certainly none in *Palaeolagus*, of the immensely hypertrophied posterior extension of the malar which is present in *Ochotona*. In this latter form, this extension is correlated with the proportionate increase in the size of the posterior branch of the *temporalis*, which is bounded laterally by this process, and which seems to have become the dominant part of the muscle in the pikas. The malar is definitely deep dorso-ventrally in all the leporids, with a clearly shown fossa for the *masseter lateralis*. This is very poorly developed in the pika, correlated with which the bone as a whole is a slender rod instead of a thin plate.

The *orbitosphenoid* is a quadrate bone as in the living leporids. As in them, the optic foramina fuse before leaving the skull, so that there is a large interorbital fenestra. This is likewise present in the pika. Posteriorly, the orbitosphenoid makes a contact with the parietal where the latter enters the orbit. The exclusion of the parietal from the orbit in Recent leporids has brought about a contact between the orbitosphenoid and the frontal

above and the squamosal below. The same is true in the pika. In the modern leporids, there is a long postero-dorsal process of the orbitosphenoid, extending between the frontal and squamosal, toward the parietal. This has replaced the corresponding process of the parietal in *Palaeolagus*, which extended toward the orbitosphenoid. There is no difference in this condition between an infant and an adult *Sylvilagus*. Anteriorly, the orbitosphenoid is bounded by the descending process of the frontal in *Palaeolagus* and *Sylvilagus*, and by the ascending process of the maxillary in *Lepus*. Ventrally, its contacts with the maxillary and palatine are similar in all three forms.

The *palatine*, as mentioned above, extends forward between the maxillaries to or nearly to P$\underline{4}$, sending a wide process forward along the mid-line. The excessive reduction of the palate which characterizes the Recent lagomorphs has taken place principally at the expense of the palatine, which extends posteriorly to M$\underline{2}$ in *Palaeolagus*, whereas in some species of *Lepus*, it extends only to P$\underline{4}$ (Dice, 1933, p. 302). "The part of the palate formed by the palatines has been especially reduced in the modern Leporidae, and, whereas in the fossil specimen the palatines form more than half the median length of the bony palate, in all modern hares and rabbits, so far as known, the palatines form less than half, and in some species they constitute only the narrow posterior edge of the palate. Among modern leporids the genus *Romerolagus* is most like *Palaeolagus haydeni* in the structure of the palate. In *Pronolagus*, also, a relatively large proportion of the bony palate is formed by the palatines. Some individuals of the domestic rabbit (*Oryctolagus*) have the palatines forming nearly half of the bony palate, but in most individuals of this genus the palatines cover a much smaller area. The palate is proportionately longer in the young of *Lepus* and *Sylvilagus* than in the adults, and in the young the palatines form a larger proportion of the palate. In this character the young resemble the primitive form." (Dice, 1933, pp. 302–303.) The pterygoid process of the palatine is long and massive, as in modern leporids, being distinctly heavier than in the pika. The pterygoid fossa extends forward well into the palatine, also as in the modern forms. The posterior nares are at the level of M$\underline{2}$, instead of being by M$\underline{1}$ as in the Recent lagomorphs. In some specimens of *Palaeolagus* (as A.M.N.H. No. 8722, the holotype of *P. intermedius*), however, the posterior nares extend as far forward as M$\underline{1}$. This may be a specific character of more progressive members of the genus. "The posterior nares are narrow in the fossil, being smaller than in any wild member of the family which I have seen. But in the domestic rabbit the air passages are as constricted as in the fossil. On account of the small size of its air passages, *Palaeolagus haydeni* could have had only weak endurance in running" (Dice, 1933, p. 304). The posterior palatine foramina are small and far forward in the bone, as in living forms, but they do not reach the maxillaries, as is the case in *Lepus*. "In the related genus, *Romerolagus*, these foramina are relatively very large, but in *Pronolagus* they are very small" (op. cit., p. 304). The dorsal margin of the palatine, within the orbit, is in contact with the orbitosphenoid. No trace of any contact with the alisphenoid could be found in any available specimen, although this area is very often broken away in the fossils. In the Recent genera, there are contacts in this region between these two bones, but the bone here is only a thin paper-like sheet, which breaks very readily.

The *alisphenoid* is always, as far as I have seen the material, broken, and is usually entirely missing. As far as could be told, however, its ventral portions are similar to those of living forms. Dorsally, however, it has a broad contact with the parietal, from which it

is separated in the living genera by the orbitosphenoid-squamosal contact. According to the reasoning of Wood-Jones (1929) with respect to primates, this would mean that *Palaeolagus* would definitely have to be removed from the line of ancestry of the Recent rabbits. Most workers would readily agree that a thesis of this sort was untenable in the absence of extremely good supporting evidence.

The *squamosal* is a large bone forming the side of the posterior part of the skull in all forms. In *Palaeolagus*, as is indicated above, it is separated by the anterior process of the parietal from the frontal. The parieto-squamosal suture is in approximately the same position in all forms. In the living leporids, there is a distinct knob at the anterior end of the squamosal, where it articulates with the frontal, apparently serving as the attachment of a ligament from the posterior wing of the supra-orbital process. This is very well marked in *Lepus*. In *Palaeolagus*, there is no trace of this knob, correlated with the much shorter supra-orbital process in that genus. Ventrally the squamosal overlies part of the alisphenoid, but in the fossil its exact relationships are hidden in all of the available specimens. Posteriorly, the squamosal reaches to the rear of the skull as in *Ochotona*, and in contrast to the Recent leporids, in which the excessive growth of the supraoccipital and mastoid has taken over the rear part of the dorsum of the skull. The squamosal of *Palaeolagus* extends posteriorly almost to the occiput and almost to the posterior end of the interparietal, with which it has a small contact. The posterior end of the bone is bounded by the occipital and the mastoid. A downwardly curved branch of the squamosal is notched into the mastoid behind the auditory meatus. In the Recent leporids, the squamosal ends entirely in front of the meatus, except for a long and extremely slender spicule of bone which runs postero-ventrad and passes just above the meatus, lying in a groove on the surface of the mastoid, and ending just behind the ear. In the pika, the squamosal does not extend so far to the rear, nor does it have the marked downward hook at the rear seen in *Palaeolagus*, nor is there any trace of the long posterior process of the later leporids. The zygomatic process of the squamosal arises near the anterior end of the bone, extending at right angles to the skull above the glenoid, as in the other lagomorphs, and then bending sharply downward to unite with the malar, forming not only the dorsal, but also the lateral, margin of the glenoid. In the living leporids, the zygomatic process does not extend far forward on the zygoma, its anterior and posterior extensions being approximately equal. In *Palaeolagus*, on the other hand, there is no posterior extension, and the anterior part extends along the upper surface of the arch nearly to the maxillary. *Ochotona* has a similar anterior extension, but the zygomatic part of the squamosal is very much more massive than in any of the other lagomorphs. Above the zygomatic process, there is a groove running posteriorly along the upper part of the squamosal, for the ventral part of the *temporalis*. In *Palaeolagus*, this groove is only faintly separated from the rest of the temporal fossa, instead of being an entirely distinct fossa as in the Recent lagomorphs. In all of the lagomorphs, fossil and Recent, the glenoid fossa is on the posterior side of the zygomatic process, instead of being on the ventral side as is more usual in mammals. This indicates the complete absence of any potentiality for antero-posterior motion of the lower jaw, and establishes the fact that if the rodents and lagomorphs have a common ancestor, that ancestor must have lived at a time prior to the establishment of the type of chewing which characterizes its descendants, and hence, presumably, before either group became adapted to a gnawing habitus.

The *bulla* is similar to that of modern leporids, but the meatal tube is not so long, nor

so straight, being curved slightly posterad at its free end. In the pika, on the other hand, there is no tube, the meatus resting directly on the bulla. The bulla is rounded and proportionately larger than in modern leporids, but proportionately much smaller than in the pika. The mastoid and paroccipital processes on its posterior face are small, as in the pika, instead of being long and squeezed into the entire posterior face of the bulla, as in modern leporids. This, of course, is merely a primitive character which *Palaeolagus* shares with the pika. The styloid process is smaller in *Palaeolagus* than in the modern leporids, and the pit for the stylohyal is very much smaller, or almost non-existent, which suggests that the hyoid was not so well ossified in the fossil as in the Recent forms.

The *mastoid* is extremely different from that of the living leporids, and closely resembles that of the pika. There is no trace of its immense expansion, which has brought it up onto the dorsum of the skull in the living leporids at the expense of the parietal and squamosal. Nor does it extend appreciably above the bulla, lying mostly behind it. It shows no trace of the fenestrations which are so characteristic of this region in Recent leporids. It extends onto the occiput in about the same manner as does that of *Sylvilagus*. In *Lepus*, the occiput has narrowed, eliminating most of the mastoid from this face. The mastoid process is widely separated from the paroccipital process, instead of being very close to it as in *Lepus*.

The *occiput* is broader and lower than in Recent leporids, approximating the conditions seen in the pika. The foramen magnum is wider than it is high, again agreeing with the pika and differing from later leporids. There is no evidence of heavy ridging of the supraoccipital for the neck muscles, indicating that these last were weaker in the fossil than in the modern forms. The strengthening of these muscles would be an adaptation for the leaping habitus of modern leporids, and their weak condition in *Palaeolagus* would suggest the entire absence of such a specialization. The occipital condyles are set at more of an angle, instead of being nearly vertical, as in *Lepus* and *Sylvilagus*. The paroccipital processes are short, not extending as far ventrad as do the occipital condyles, a primitive character in which *Palaeolagus* agrees with *Ochotona*, whereas the other genera have progressed beyond this point. The basioccipital is much more highly keeled than is the case in any of the other three genera of lagomorphs compared. There are distinct lambdoid crests, entirely absent in the modern leporids, though present in *Ochotona*, marking the boundary between the dorsal and occipital sides of the skull.

Cope (1884, pp. 873–874) gives a detailed description of a brain cast which he referred to *Palaeolagus*. If this specimen should belong to this genus, it shows striking differences from the brain of the living leporids, particularly in the immensely larger size of the olfactory lobes, as Cope pointed out. The hemispheres are smaller than in living leporids, and their fissuring is further advanced. There are no traces of skull attached to this specimen at present which could assist in identifying it. It is possible that they were once preserved, and removed by Cope before the description of the specimen, and that his identification of this fossil as *Palaeolagus* was based on such skull fragments. The least width of this brain cast, between the hemispheres and the olfactory lobes, is considerably greater than the interorbital width of the skull of *P. intermedius*, the largest species of *Palaeolagus*, and the cerebral hemispheres are too small to fill the cranium of that form. Hence it is concluded that this specimen is not the brain cast of a lagomorph, although there might be a faint possibility that it is the brain cast of *Megalagus* or *Desmatolagus*, since the skulls of these genera are unknown.

In summary, the skull of *Palaeolagus* resembles that of the modern leporids in many characters, and is typically that of a leporid, showing no approaches to any non-lagomorphine stocks. The many differences between *Palaeolagus* and its Recent relatives are merely instances in which the fossil is more primitive, and are no greater than would be expected in view of the time that has elapsed since the Oligocene. There are numerous points in which *Palaeolagus* agrees more closely with *Ochotona* than with the other Leporidae. These have been interpreted as being resemblances to the primitive lagomorph type, which have been lost in the later leporids largely because of their saltatorial and cursorial specializations. There is no evidence, however, for any special relationship between *Palaeolagus* and the ochotonids, and it is believed that the two lines have been divergent at least since the lowest Upper Eocene, in view of the fact that the Uinta *Mytonolagus* appears already to have been a true leporid.

The *mandible* is much more primitive in certain respects than is that of the living members of the order. There is a distinct coronoid process, nearly as high as the condylar process. The ascending ramus rises abruptly opposite the middle of the last molar. In the Recent genera, there is only a faint trace of a coronoid, far down on the anterior side of the ascending ramus. The anterior and posterior sides of the ascending ramus are essentially parallel, instead of converging posteriorly toward the condyle as in the living forms. The condyle, viewed from above, is comma shaped, with an anterior knob extending into a narrow posterior crest. This is accentuated in the later genera. This anterior knob is the part that actually articulated with the glenoid fossa of the squamosal. The anterior face of the ascending ramus is grooved in all forms for the insertion of the *temporalis*. The broad plate of the posterior part of the mandible has been strengthened peripherally, but has not yet been reduced to the paper-thin medial sheet that is found in Recent rabbits. The ventral border of the masseteric fossa swings up onto the lateral face of the mandible, and ends anteriorly in a small knob, below $M\overline{3}$. In Recent rabbits, the ventral border of the fossa does not make such an even curve. In the pika, the fossa is not extended below the level of the rest of the ramus. The posterior margin of the ascending ramus is an even curve, instead of being rendered asymmetrical ventrally by the upgrowth of the dorsal part of the angle. This upgrowth appears to have been to furnish a greater surface for the insertion of the masseter, and a stronger point of insertion for the *pterygoideus*, correlated with increased chewing efficiency in the later members of the family. "The posterior part of the mandible, though well provided with space for the attachment of the masseter muscles, is not nearly so well developed as in the hares of the subfamily Leporinae. The lower border of the mandible has no important downward development in the hinder third, as is true of *Lepus*, *Sylvilagus*, and their relatives. The mandible of *Romerolagus* is closely similar to that of the fossil, differing chiefly in being somewhat larger and in having the vertical ramus higher in proportion to the length of the mandible. On the other hand, the mandible of *Alilepus annectens*, which I have also placed in the subfamily Palaeolaginae, is much more like those of the Leporinae in type. . . . The posterior part of the mandible of this genus has a pronounced enlargement, such as is found in *Lepus*" (Dice, 1933, pp. 304–305). The ramus of the mandible is essentially similar in all members of the family, though Burke states that that of *Mytonolagus* is somewhat lighter throughout than is that of *Palaeolagus* (1934, p. 410). In all forms, it is heavier than in *Ochotona*. A few nutritive foramina are present in the ramus of *Palaeolagus*, though nowhere near as many as in

*Sylvilagus*. There are always "two mental foramina, one on the middle of the depth of the ramus, below the fissure between the second and third molars [$P\overline{4}$ and $M\overline{1}$]; and the other, marking the posterior third of the diastema, near its superior border" (Cope, 1884, p. 876). The mental foramen is not as high on the side of the mandible as in *Sylvilagus*. The alveolar border is continued through the diastema as a sharp ridge. This is a characteristic feature of all the Leporidae. The incisors are not as procumbent as in the modern rabbits, a more primitive condition, and one suggestive of a complete absence of all burrowing habits. This form differs from *Mytonolagus* in that in the latter form "the course of the incisor diverges less from the plane of the ramus. The incisive swelling is less prominent and extends back under $M\overline{2}$, but the incisor does not reach posteriorly beyond the anterior root of the latter tooth" (Burke, 1934, p. 410).

The *masseter muscle* appears to have undergone but little change from the Oligocene to the present, merely expanding the area of its insertion and strengthening the attachments at its origin. The *temporalis*, on the other hand, appears to have changed considerably. With this change is associated a considerable part of the modifications of the posterior part of the skull. The backward growth of the supra-orbital process was beginning to crowd the *temporalis* in *Palaeolagus*. This growth pinched the muscle, eventually dividing it into two sections. That there was already the tendency toward such a subdivision in *Palaeolagus* is indicated by the faint suggestion of a separation of the temporal fossa into two parts in that form. The ventral part of the muscle, which lies along the squamosal in *Palaeolagus*, was eventually separated from the dorsal part, and progressively developed a more and more antero-posterior pull. As the pinching of the dorsal part of the muscle by the supra-orbital process continued, this ventral section became more and more important, until in the Recent forms, this is the major part of the muscle, and the main function of the *temporalis* is to pull the mandible backward. From this it would appear that, in the living forms, the *temporalis* is used primarily in gnawing, the chewing being performed by the masseters and pterygoids. These last muscles, of course, are also used in gnawing.

The *upper incisors* differ but little from those of the living forms. There is no indication in these teeth in *Palaeolagus* of an approach toward a prelagomorph type of incisor, as Matthew has already remarked (1902, p. 307). The anterior incisor agrees with that of the more primitive Recent genera. The sulcus, though pronounced, is simple, with no trace of the enamel folding into the complicated pattern seen in some species of *Lepus* (Forsythe Major, 1899, p. 468, Figs. I–XXIV). The incisor of lagomorphs in general differs from that of the rodents in being a larger arc of a much smaller circle. *Palaeolagus*, in this respect, is nearer to the rodents than are the later genera, though even here there is a sharp difference from all known rodents. The incisors grow in such a manner that their tips point directly downward, with no trace of the slight procumbency seen in *Lepus* and *Sylvilagus*. By analogy with the rodents, this indicates that the gnawing function was more highly developed in *Palaeolagus* than in the Recent genera. The posterior upper incisor is proportionately large, being only slightly smaller in cross section than is the anterior one. It is, in fact, almost as large absolutely as the corresponding tooth in the much larger *Lepus*. Nothing in the incisors of any specimen of *Palaeolagus* that I have seen gives any indication as to which one of the normal mammalian three upper incisors has been lost. It is very probable that the two incisors that remain are either $I\underline{1}$–$\underline{2}$ or $I\underline{2}$–$\underline{3}$. Since the lower incisor bites between the two upper ones, it would seem very likely that the lower

tooth is either $I\frac{2}{2}$ or $I\frac{3}{3}$, depending on which of the two alternative interpretations of the upper teeth is correct. $I\frac{1-2}{2}$ would seem the most logical interpretation. In all known forms, the incisors are ever-growing.

In the following discussion of the *premolars*, it has been assumed that the series $P\underline{2} \rightarrow dP\underline{2} \rightarrow P\underline{3} \rightarrow dP\underline{3} \rightarrow P\underline{4} \rightarrow dP\underline{4}$ is one of increasing specialization. This is the normal condition in mammals, and, until the contrary can be established, should be assumed to be the actual situation in the lagomorphs. From all the available evidence, it could equally well be assumed that the series runs in the opposite direction, with increasing simplification, if this interpretation should happen to fit in better with one's preconceived ideas of lagomorph dental evolution. More detailed discussions of the significance of the tooth pattern of these premolars will appear on a later page (see below, p. 351).

The small buccal roots that are present in the permanent upper cheek teeth of *Megalagus* and *Desmatolagus* do not occur in *Palaeolagus*, the support of the crown being entirely taken over by the hypertrophied internal portion of the crown. If one desires, this could be called a root, though actually the root does not develop until the animal has attained an extreme old age, particularly in the Brulé forms.

$P\underline{2}$, when unworn, is one of the simplest of all rabbit teeth. It is a trefoil (Figs. 71 and 79), with the three lobes united into a marginal crest along the posterior side of the tooth. Burke's figure of this tooth in *Mytonolagus* (1934, Pl. L, Fig. 1) suggests that in that form the three lobes may have united directly with each other, and that in *Palaeolagus* they have moved slightly apart, the crest arising as the cusps separated. In unworn teeth, the central lobe extends farthest forward and the lingual one is slightly the largest. Due to the buccad curve of the groove between the outer two cusps, progressive wear increases the size of the central cusp at the expense of the buccal one. Finally, the groove between the buccal and central cusps is entirely worn away, and the only indication of the former is the slight irregularity on the posterior margin of the tooth, which, in turn, also soon disappears. At this time, the tooth has attained the pattern used by Dice (1917, p. 180) as characteristic of *Archaeolagus*. The pattern of this tooth in *Palaeolagus* is quite different from that in *Mytonolagus*. Of the latter, Burke states: "The principal lobe . . . is central, elongate longitudinally and produced anteriorly beyond the external and internal lobes. The internal lobe . . . is the smallest of the three and separated from the central lobe anteriorly by a longitudinal valley. Postero-external to the central lobe occurs a third lobe . . . separated from the paracone anteriorly by a narrow valley which takes a postero-external course toward the posterior wall" (Burke, 1934, pp. 401–402). That is, in *Mytonolagus*, the lingual lobe is much smaller than in *Palaeolagus*, and is directed much more linguad rather than antero-linguad as in the latter form. The buccal lobe is proportionately larger, particularly after a considerable amount of wear (Burke, 1934, Pl. L, Fig. 1). That is, between *Mytonolagus* and *Palaeolagus*, there has been a progressive reduction of the buccal lobe and enlargement of the lingual one. The significance of this modification will be brought out more fully below. In *Palaeolagus*, there is no trace of any subdivision of the intra-alveolar part of the tooth into two columns, an advance over *Mytonolagus*. "$P\underline{2}$ may be described as having but a single root, but a strong vertical groove on the antero-external side of this root above and between the [central and buccal] . . . lobes indicates a bi-fanged history. I find a groove similarly placed in $P\underline{2}$ of a specimen of *Desmatolagus*

*gobiensis* . . . , but in the latter tooth the groove is more prominent. In both cases the root shows a cross-section at the base similar to that observed by Forsythe Major in P3 of a specimen which he refers to *Titanomys visenoviensis* . . ." (Burke, 1934, p. 402).

P3 begins life as a distinctly more complicated tooth, though still fundamentally three lobed. All the elements that were visible in P2 are clearly discernible here, but to them are added a number of complexities. One specimen was fortunately discovered showing this tooth entirely unerupted. At this time the antero-posterior diameter of the tooth is actually greater than it becomes after further wear (Fig. 80). This, together with the fact that the transverse diameter is much less than in worn teeth, gives the tooth an appearance quite different from what is usually expected in *Palaeolagus* upper premolars. The lingual of the three lobes is tremendously hypertrophied, and, possibly because its anterad expansion was prohibited by the presence of P2 immediately to its front, the distal end of the lobe has swung buccally in front of the central lobe. This is a striking advance over the slightly worn tooth in *Mytonolagus* (Burke, 1934, Pl. L, Fig. 10), where the lingual lobe extends but slightly anterad of the central one. The unworn tooth in *Palaeolagus* is in the same evolutionary stage as the considerably worn P3 of *Mytonolagus* (op. cit., Pl. L, Fig. 1). On the other hand, in an unworn specimen of *Mytonolagus*, the lingual lobe "extends across the anterior face of the crown, descending to the antero-external angle to meet the spur" from the buccal lobe (Burke, 1934, p. 403). This variability may merely indicate the initial stage in the development of the anterior lobe, or it may corroborate Burke's first impression that more than one species is represented in the Uinta material (op. cit., p. 400). Burke further states: "I believe that no particular stress can be placed on the variations seen . . . in P3 of this species. [The buccal lobe] . . . also appears to show considerable variation in *Palaeolagus brachyodon* . . . and in *Desmatolagus gobiensis* . . . ; Walker describes a condition which seems to resemble that found in C. M. 11935 as characteristic of P3 of *Palaeolagus turgidus* . . . , but in all the specimens of P3 of *Palaeolagus turgidus* . . . which I have seen, in which wear had not eliminated the pattern showing at the crown surface, I have detected only one reëntrant in this region, the antero-external" (op. cit., p. 403). Walker is rather vague in the description of this tooth to which Burke referred, stating that: "Upper pre-molar 3 is characteristic of this genus, being oval in outline, with two anterior re-entrant angles, separated by a median ridge. Both appear to be of nearly the same depth, and do not extend as far as half way across the crown" (Walker, 1931*b*, p. 234). He does not illustrate this tooth. This description is so general that it could apply to a pattern such as that in *Desmatolagus* (see below, Fig. 111) or *Megalagus brachyodon* (Fig. 106), just as well as to the pattern Burke shows (Pl. L, Fig. 10). So, until other evidence is adduced, it seems best to take the position that that particular tooth which Burke figured has a pattern unique among the leporids. In *Palaeolagus*, slight irregularities have begun to develop in the outline of the lingual lobe, though only one is apparent in the unworn teeth. This, the most important, is at the postero-lingual side, where a strong groove, running the entire height of the crown, divides this part of the tooth into two parts, which would normally be, and have generally been, called the protocone and hypocone. The central lobe has undergone little change from the conditions in P2. It has, however, begun to elongate, and since the free end of the lingual lobe limits its anterior expansion, it has begun to curve, and the free tip has extended toward the buccal margin of the tooth. The buccal lobe is distinctly enlarged by outgrowths to form three lobules (Fig. 73), which

are just beginning to develop in *Mytonolagus*, Burke stating that the main part of this lobe "is attenuated anteriorly into a long spur which curves around the antero-external angle of the crown. Posterior to . . . [this lobe] occurs a tiny transverse enamel notch, almost isolated as an island" (Burke, 1934, pp. 402–403). One of these lobules runs toward the posterior or attached end of the central lobe. The two others have grown outward from the anterior and posterior corners of the buccal lobe, and then bent toward each other. None of the figured specimens shows this part of the tooth clearly in an early stage of wear. The same stage in pattern development is illustrated, however, in the figures of P$\underline{4}$ and dP$\underline{3}$ (Figs. 73–75). These lobules may represent elevated cingula, or may merely be indicative of a tendency toward extravagant growth of crests, similar to that observable in *Eutypomys* (Wood, 1937*b*, Figs. 40–45). The space which these lobules surround, as well as all of the valleys between the lobes, is filled with cement in erupted teeth. The cement appears to be deposited immediately before the tooth pierces the gums, but after it has erupted from the alveolus. As wear progresses, the distal end of the lingual lobe extends progressively farther buccad, so that in worn teeth this lobe forms the entire anterior side of the tooth. The lingual one of the three lobules of the buccal lobe is of greater extent, also, in the rootward portions of the tooth, and extends farther and farther forward, eventually forming the entire anterior half of the buccal side of the tooth, meeting the distal end of the lingual lobe. The central lobe is thus eventually cut off entirely from the margins of the tooth by the growth of the other two lobes. This is a striking advance over *Mytonolagus*, in which "an anterior 'wall' . . . extends toward the external side of the crown but does not entirely subtend the anterior horn of the . . . [central lobe] from the anterior face of the tooth" (Burke, 1934, p. 402), much less separate it entirely from the buccal margin. The cement lake at the postero-lateral margin of the tooth, between the lobules of the buccal lobe, quickly disappears, being followed soon after by the lake between the two outer lobes. At this stage, the only cement lake left is that between the central and lingual lobes. Due to the buccad growth tendency of the central and lingual lobes, this lake is V-shaped, and appears to be the homolog of the V in the molars. The next stage in wear is the separation of a small lake from the closed end of the fold between the "protocone" and "hypocone" and the reduction of the fold to a shallow groove on the lingual margin of the tooth. Some time before this happens, however, the enamel organ ceases the deposition of enamel on the buccal side of the tooth, so that with slightly further wear the crown is surrounded by enamel on three sides only. The elimination of the enamel does not occur until practically the entire buccal side of the crown is worn away. Due to the marked asymmetrical hypsodonty, the lingual part of the tooth is still actively growing at this time. As the break in the enamel first appears in the center of the buccal side of the tooth, a notch is developed there. The next stage is the elimination of the hypostria, leaving the central V-shaped lake and the small hypostria-lake. The latter in turn soon disappears. At this stage, the pattern is similar to that of the diplotype of *Mytonolagus* (Burke, 1934, Pl. L, Fig. 1), except that the V is retained much longer in that form, which is one of the primitive characters of that genus. Subsequent to this, the peripheral enamel is gradually reduced in extent, till, in the oldest specimens that I have seen, it surrounds only the lingual half of the tooth.

P$\underline{4}$ represents a very much more advanced stage in this same sequence. The anterior lobe is extended, and reaches the buccal margin of the tooth, being about as long buccolingually as is the posterior half of the tooth (Fig. 80). It has apparently encountered the

free end of the central lobe and carried the latter along with it, so that they both reach the buccal margin of the tooth, making the central lobe V-shaped. This tooth in *Mytonolagus* is distinctly more primitive than in *Palaeolagus*, the central lobe showing only the slightest trace of the bend in its middle which becomes so pronounced in *Palaeolagus* (Burke, 1934, Pl. L, Fig. 10). In *Palaeolagus*, the two lobes are so close to each other that, even in entirely unworn teeth, no separation is visible between their buccal portions (Fig. 80), a distinct advance over *Mytonolagus* (op. cit., Pl. L, Fig. 5), where "the outlet of the valleys at the antero-external corner of the crown is open nearly to the base" (op. cit., p. 404). While this has been going on anteriorly, a small lobule of the buccal lobe has grown forward, and, after a limited amount of wear, unites with the combined internal and central lobes, closing the buccal border of the tooth, and separating a buccal valley, which lies on the crown as an enamel lake. The two postero-buccal crests of the outer lobe have also expanded and united, developing another lake in the extreme postero-buccal angle of the tooth. While the lobes have been modifying themselves in this manner, equally important changes have manifested themselves in the valleys of the tooth. The hypostria is of considerably greater depth than in P3, due largely to the increase in the transverse diameter of the tooth by the inward growth of the "protocone" and "hypocone," and is directed more nearly toward the lunate valley, which represents the space which formerly existed between the central and lingual lobes (Fig. 79). "The greater development of the internal groove in the premolars of *Palaeolagus haydeni* Leidy as compared with the corresponding teeth in this species [*Mytonolagus*] should not, in my opinion, be taken as an indication of the rate of evolution of this character in the early Leporidae. It is not only in *Palaeolagus haydeni* Leidy, but also in *Palaeolagus temnodon* Douglass and in *Palaeolagus agapetillus* Matthew (*non* Cope), that we find the more transverse type of internal notch in the premolars, comparable with the incipient '*Lepus* pattern' of the molars. On the other hand, the internal notch in the premolars of *Palaeolagus brachyodon* Matthew cannot be said to be much more pronounced than that seen in *Mytonolagus petersoni*" (Burke, 1934, pp. 404–405). P4 is distinctly molariform, the only permanent upper premolar of *Palaeolagus* in which this is the case.

The *milk premolars* form a series which, in specialization, integrates completely with that of the permanent premolars. DP2 (Figs. 73 and 82) is much more complicated than P2, approaching P3 in this respect. The internal lobe is distinctly longer than either of the others, and is separable into three lobules by the hypostria and by a groove on the buccal face of the lobe. The distal lobule has reached a point anterad of the central lobe, and is beginning to swing buccad. This is clearly shown by the valley between the central and lingual lobes, which is no longer essentially straight as in P2, but has a distinct buccad curve. The fact that the lingual lobe is curving toward the outer side in this tooth, which has no other teeth in front of it, indicates that the similar curve in P3 is not entirely due to a lack of space caused by the presence of another tooth in front of it. The central lobe shows no features of note other than a slight lengthening and a faint trace of a buccad curve in the free tip. The posterior crest is somewhat elongate, and the space between the central and lingual lobes is increased. The buccal lobe has developed a concave outer surface, the initial stage leading toward the development of the two buccal arms which are present in P3. The shape of the tooth is subtriangular, almost halfway between that of P2 and that of P3.

DP3 shows a pattern again intermediate between its successor, P3, and the permanent tooth next in line, P4. The lingual lobe is elongate and reaches the buccal margin of the

tooth, though it does not extend quite as far as does the buccal lobe, a feature which characterized P3 as well. In this respect, it is in almost the same stage of evolution as P4 of *Mytonolagus* (Burke, 1934, Pl. L, Fig. 5). The hypostria is increased in depth, and the "protocone" and "hypocone" are clearly set off from each other, an advance over any of the ante-molar teeth of *Mytonolagus*. There are suggestions of several cuspules in the anterior arm of this lobe, which only show up in the early stages of wear. The space between the lingual and central lobes along the posterior margin of the tooth is much increased, so that the lunate valley formed between the two lobes has anterior and posterior arms of nearly equal length, a striking contrast to conditions in *Mytonolagus* and *Desmatolagus*, and, to a lesser extent, to those in *Megalagus*. The central lobe now arises from the buccal border of the tooth, runs linguad, and then bends around almost parallel to its former course, reaching the buccal border of the tooth just posterad of the tip of the lingual lobe. A cusp-like swelling of this central lobe comes very close to the buccal end of the lingual lobe, on the one hand, and to the buccal lobe, on the other, marking an approach to conditions in P4. Although the central lobe reaches farther buccad than does the lingual one, it does not extend as far as does the buccal one. This last is a rounded mass, surrounding an enamel lake formed by the union of its buccal arms. A small lobule is extended forward, nearly meeting the central lobe, and almost closing the buccal end of the central valley.

DP4 is in some respects less advanced than either dP3 or P4. It is quadrate as are P4 and the molars, but has less of the antero-posterior compression of the molars than does P4. This may be because, due to its brachydonty, dP4 does not have time to attain the compression reached by the permanent teeth in the later stages of wear. The hypostria is better developed than in any other premolar. In unworn teeth, the lingual lobe does not extend quite as far buccad as the central one, though after slight wear the reverse is the case (Fig. 73). Burke's figure of this tooth in *Mytonolagus* (1934, Pl. L, Fig. 6) shows this tooth at the stage where the two lobes are of equal length. In *Palaeolagus*, these two lobes are very close together, so that but little wear is needed to unite them (Fig. 82). In this character, this tooth is entirely molariform. The valley between the central and buccal lobes is much more widely open than in either dP3 or P4, and the lake of the buccal lobe is less well developed than in the other teeth. In this *Palaeolagus* agrees exactly with *Mytonolagus*. The whole buccal lobe gives the appearance of being reduced and simplified, and it is only with difficulty that the various parts can be made out. The posterior marginal crest is entirely separated from the central lobe, which arises from the buccal lobe, again exactly repeating the conditions seen in *Mytonolagus*. In the Uinta genus, the hypostria is directed backward, as in the molars, so that the hypostria lake develops behind the midline of the tooth rather than on it, as in *Palaeolagus*. This is a striking difference, indicating closer relationships between *Mytonolagus*, *Megalagus* and *Desmatolagus* than between any one of those forms and *Palaeolagus*.

The best analysis that I have seen of what takes place during the evolution of rabbit upper *molars* is given by Forsythe Major (1899, pp. 452–453), speaking of *Prolagus*. It is, however, equally applicable to all other lagomorphs. "The outer parts of the crown, those which are least affected by trituration, have degenerated in consequence of disuse; and we might be inclined to assume that compensation has been effected by the transverse fold penetrating towards the outer part. But this is not, to all appearance, the exact explanation of the phenomenon. The triturating surface in the tooth of the young animal—in the part

of the shaft which is earliest formed—is more square than in the adult; in the latter, it presents the well-known narrow transverse shape of the lagomorphine upper molar. If we remove one of these teeth from its socket and examine it from the anterior or posterior side, it can be seen that, while its outer border maintains throughout its height almost a vertical direction, or is even concave, the inner part of the tooth slopes down medially, from below to above. . . . The tooth, therefore, as it continues to grow, extends persistently in a transverse direction; but this growth takes place chiefly, if not exclusively, towards the internal side; so that the transformation of the internal notch of the *Titanomys*-tooth into the transverse fold of the true molars of *Prolagus* is not the result of its extension outward but inward. In other words, new formation takes place in that part of the tooth where there is increased work, while the outer part—that which is scarcely or not at all affected by trituration—not only remains stationary, but even becomes atrophic." Whatever the underlying causes may be, this is certainly an accurate description of the changes that occur.

The two anterior molars show a pattern closely resembling that of the two posterior premolars, giving every indication of having been derived from the same fundamental pattern in the same manner. Troxell's figures show this similarity well (Troxell, 1921, Figs. 9–16). His discussion gives the impression that he thought the two sets of teeth fundamentally similar. Ehik (1926, pp. 179–180) definitely states that he considers that the molars are based on the same pattern as are the premolars. Burke (1934, pp. 407–408) likewise states that the premolars and molars had the same ground pattern. What the fundamental pattern of either the molars or premolars may be will be discussed in more detail below (pp. 351–354). Although it is quite possible that basically the two sets of teeth have entirely different patterns, nevertheless the posterior premolars have so completely attained the same pattern as is exhibited by the molars that it would seem only reasonable to assume that fundamentally they are the same.

In slightly worn, or erupted and unworn, molars (see Figs. 71, 72, 78 and 81), there is an elevated crest along the anterior margin of the tooth, continued at right angles half way across the lingual side of the tooth. Behind this crest, and forming the hypotenuse of a triangle the other sides of which are the two arms of the crest, is a broad shelf. This triangle, after further wear, forms a broad dentine surface. This is what Burke (1934, p. 407) has called the protocone, or perhaps the protocone and protoconule. The posterior wall of the tooth is an elongate, narrow crest, which extends forward on the lingual margin of the tooth to end in a swelling, the hypocone, separated from the protocone by the deep hypostria. The buccal part of this posterior crest is what Burke considers a degenerate metacone. The central part of the tooth is occupied by a crescentic cusp, which Burke calls the paracone (1934, p. 407). On the buccal edge of the crown are a variable number of small cuspules, which he thinks of little phylogenetic significance (op. cit., p. 406). Certain of these external cuspules, however, I believe to be of considerable importance, representing the posterior arm of the central lobe at the point where it arises from the posterior lobe. In order to see this feature with absolute clarity, it is necessary to have not only unworn, but also unerupted teeth, since slightly before eruption a thick coat of cement is deposited over the crown, which completely masks the details of the pattern (compare Figs. 78 and 81). For the present, no attempt will be made to determine the homologies of the different parts of the molars, this being reserved for a later place (see below, pp. 353–354).

In unerupted molars in which the pattern has neither been simplified by wear nor

masked by the deposition of cement, the pattern of M1–2 is extraordinarily like that of P4. The premolars and molars are emplaced in the maxilla at slightly different angles, so that they are worn at different angles, and hence worn teeth lose their appearance of fundamental identity. There is quite a lot of difference between these teeth in *Palaeolagus* and in *Mytonolagus*. There is a crest running almost continuously along the anterior, lingual and posterior faces of the tooth, notched in the middle of the lingual side to form a ⋀ (Figs. 72 and 81). From the tip of the notch, subsidiary crests run across the internal angles to the anterior and posterior sides, serving, apparently, as flying buttresses to strengthen the crown. The spaces between these buttresses and the marginal crest are slight valleys. Upon wear, these valleys disappear entirely, their places being taken by broad dentine surfaces, which are commonly referred to as the "protocone" and "hypocone." The parts of the unworn tooth that appear actually to be the protocone and hypocone, if the homologies used in this paper are correct, are really only the extreme lingual portions of these dentine surfaces. At the buccal side of the tooth, the free ends of the ⋀ often unite with the corresponding ends of the external crescent or V, which appears to correspond to the central lobe of the premolars. The ⋀ would then correspond to the buccal lobe, posterior crest and lingual lobe of the premolars. This seems to be almost the identical pattern that occurs in P4, though whether or not it was attained in the same manner can not be told at the present time. This condition is shown in Figs. 72 and 81. In many other specimens, however, only the anterior arm of the crescent unites with the free ends of the ⋀, the posterior arm of the V being greatly shortened (Figs. 71 and 78). This gives a picture which suggests that the anterior side of the molars corresponds to the posterior side of the premolars, and that the free posterior end of the V in the molars is the equivalent of the free anterior end of the central lobe of the premolars. Of course, it is not at all reasonable to assume homologies of this sort, but there is a strong suggestion that, whatever the fundamental pattern, the molars and premolars have developed to a point where they are mirror images of each other.

The first thing that happens with wear is the loss of their identity by the buttresses. Then the buccal valley of the V is closed by the union of rounded extensions from the free ends of the two arms. The lake so formed is very ephemeral. In those individuals in which the posterior arm of the V is shortened, the valley is closed by the union of the anterior arm of the V with the posterior arm of the ⋀, and the buccal lake is a hook attached to the posterior tip of the crescentic lake. After the buccal lake disappears, the buccal crescent grows rapidly in size and fuses more strongly with the anterior and posterior arms of the ⋀. When this happens, the tooth has lost all trace of its initial cuspate and lophate character, and has become almost a peneplain, with dentine and cement filled depressions slightly overtopped by enamel ridges. The linguad growth of the inner part of the tooth, in the manner described by Forsythe Major, continually increases the length of the lingual fold until fairly late in life. After wear has proceeded to the point where the fold no longer gapes widely lingually, but when the two sides have become essentially parallel, there intervenes a short period of time when there are distinct crenulations along the sides of the fold. Only a small amount of additional wear is needed to get below the zone of crenulations into a region where the sides of the valley are smooth and straight. It is possible that this fact is of considerable phyletic significance. Normally, the biogenetic law seems to apply quite well to tooth development. The unworn crown shows the nearest approach to the ancestral

condition that is visible in any stage of the animal's lifetime. Frequently, this is masked by later superpositions, but with care the ancestral pattern can be made out. An example of this is in the case of *Eutypomys*, where the primary cusp pattern can be clearly seen only in unworn teeth, since in slightly worn ones the anastomosing crests complicate the situation to the point where nothing can be told of the fundamental ground plan of the tooth (Wood, 1937*b*, pp. 224–226 and Figs. 40–45). Since the unworn crown shows the most primitive stages of the crown pattern, it follows that worn patterns would represent more advanced stages. It has been my experience in studies of the more hypsodont rodents that, as a tooth is worn down, its pattern parallels the evolutionary stages that have been passed through with very considerable exactitude. If this same rule should hold true for lagomorphs, the fact that the molars of *Palaeolagus* pass through a stage in which the hypostria is crenulated and then enter a stage in which its walls are smooth, suggests the possibility that *Palaeolagus* may be descended from an ancestor in which the crenulations persisted throughout life, and hence that *Palaeolagus* definitely represents a side branch from the main evolutionary line of the Leporidae, since crenulations throughout most or all of the animal's life characterize the higher leporids. This would further imply that *Archaeolagus* and *Hypolagus* could not be ancestral to *Lepus*, a conclusion reached by Gazin (1934, p. 114) on other grounds. Whatever the facts may be about the relationships of *Palaeolagus* to the other leporids, these crenulations undoubtedly are an important key to the analysis of rabbit relationships.

In the more primitive species, after the loss of the crenulations, the buccal end of the valley is cut off from the lingual end to form a circular enamel lake which persists for a short time, during which the hypostria rapidly decreases in length. At the same time that these changes in the hypostria have been taking place, the enamel fold between the central and lingual lobes has been steadily decreasing in size, and it disappears shortly before the loss of the lake formed from the hypostria. About the time that the crenulations of the hypostria are worn away, the enamel is lost on the buccal margin of the tooth. This naturally weakens this portion of the crown, and results in an increasing rate of wear, which soon wears through the overhanging buccal part of the tooth, and leads to extensive modifications of the shape of the outer part of the crown. In advanced old age, the enamel only surrounds the lingual half of the tooth, which has lost all its lakes and all trace of the hypostria.

M$\underline{3}$ has suffered considerable reduction in size and there has been considerable simplification of the pattern of the crown, so that its details can be determined only with difficulty, even in unworn teeth. There is an anterior crest, which appears to be homologous to the corresponding crest in M$\underline{1}$–$\underline{2}$. The posterior crest appears from a specimen of *P. temnodon* (Fig. 78) to be homologous to the central crest of the other molars. In *P. haydeni* (Fig. 72), this tooth has been modified to such an extent that it no longer shows any especial resemblance to the other molars, but is merely a U-shaped crest, with the opening postero-linguad. M$\underline{3}$ does not show the minor features visible in the other teeth, even when entirely unworn. In *P. temnodon*, the posterior crest is overlapped by the anterior one at both ends, and, lingually, an arm of the anterior crest even extends behind the posterior crest (Fig. 78). With wear, these two crests soon unite, first at the buccal side, so that the unworn pattern in *P. haydeni* seems to be the equivalent of the worn pattern of *P. temnodon*, as would naturally be expected. Sometimes the posterior crest in *P. temnodon* appears to be divided into two cusps, one of which unites with each end of the anterior crest. At any

rate, there is an exit from the central valley which sometimes passes directly posterad, as if through the middle of the posterior crest, and sometimes trends postero-mesiad, on the lingual side of that crest. After a very brief time, the opening is closed, leaving a central lake surrounded by a continuous loph. A small posterior cingulum may extend along the posterior side from the lingual end of the anterior loph, but it is soon worn away. After a very limited amount of wear, this tooth is reduced to a single circular column of dentine surrounded by enamel, and with no traces of any pattern. This tooth has been so much simplified in the course of its reduction that it is not able to pass through the same wear stages as are followed by the other two molars. No trace has been seen in *Palaeolagus* of the detailed pattern described by Burke (1934, p. 409) for this tooth in *Mytonolagus*.

The general molar pattern of *Palaeolagus* appears to be somewhat different from that of *Mytonolagus petersoni* as indicated by Burke's figures and description. In *Mytonolagus*, the internal fold is much deeper and extends in a more transverse direction than in *Palaeolagus*, and reaches from a third to two fifths of the way across the tooth. The lake in $M\underline{1}$ of Carnegie Mus. No. 11,935 (Burke, 1934, Pl. L, Fig. 10) is quite clearly the buccal margin of the internal fold. The similar lake in *Desmatolagus* (Burke, 1936, Figs. 6–7) is shown by Matthew and Granger's figure (1923, Fig. 10A, $M\underline{2}$) likewise to be a separation of the buccal end of the hypostria. The unworn molars of *Palaeolagus* show that this fold was by no means as extensive in this genus, and there was no trace of the backward curve to its closed extremity. In *Palaeolagus*, moreover, the crescentic lake connects with the buccal margin of the tooth behind the central lobe, instead of in front of it, as in *Mytonolagus* and *Desmatolagus*. This definitely corroborates Burke's remark (1934, p. 405) that *Mytonolagus* is more closely related to *Megalagus* than to *Palaeolagus*.

The *lower incisor* is a broad, flat tooth, quite similar to that in the modern leporids, and distinctly different from that in *Mytonolagus*, which "is more slender than that of *Palaeolagus haydeni* Leidy, and does not show the tendency toward a flattened anterior face seen in the White River species" (Burke, 1934, p. 410). There are no traces of any grooves or irregularities in the enamel on its anterior face. It extends under the lingual part of the premolars, and grows from a persistent pulp which forms a knob on the lingual side of the mandible below $M\bar{1}$, or between $M\bar{1}$ and $M\bar{2}$. This is, nevertheless, a longer incisor, proportionately, than that in modern leporids, where the pulp lies on the lingual side of the mandible anterior to $P\bar{3}$. That is, there has been a very marked proportionate reduction in the length of the lower incisor since White River time, and, as indicated above (p. 289), perhaps a slight reduction between Uinta and White River. The most obvious explanation of this reduction is that the growth of the prisms of the lower cheek teeth interfered with the functioning of the enamel organ of the lower incisor, and that, following the path of least resistance, the latter migrated forward. As a result of this shortening, the lower incisors of living leporids are more curved than are those of *Palaeolagus*. This is very interesting and significant when compared with the conditions in *Eurymylus*, where the lower incisor is even longer than in *Palaeolagus*, extending at least to beneath $M\bar{2}$, and possibly farther. Assuming, for the time being, that *Eurymylus* was a lagomorph, this suggests that the gliriform dentition developed early in lagomorph history, that the incisor reached its full development at a time well back in the Paleocene or Cretaceous, and that subsequently the development of hypsodonty in the cheek teeth has resulted in a continual shortening of the lower incisor. *A priori*, this explanation appears fairly reasonable and it is certainly in accord with all the known facts, including the conditions in *Mytonolagus*.

The unworn permanent *lower teeth* consist of two main lobes and a subsidiary posterior lobe. The relationships of these are shown in the figures (Figs. 74, 76, 84, 85 and 86). In these teeth, the part of the crown actually showing the pattern has become greatly reduced in height, and the rest of the crown has become exceedingly hypsodont, so that the pattern is even more evanescent in the lower cheek teeth than in the upper ones. The presence of an extensive deposit of cement aids in the concealment of the fundamental crown pattern. It has generally been assumed, probably correctly, that the anterior of these lobes is the homolog of the trigonid, and the posterior of the talonid, of normal mammals, with the third lobule either a hypoconulid or a posterior cingulum, more probably the former. There does not appear to be any conclusive evidence as to the exact nature of this lobule at present. The general appearance of the teeth strongly suggests that these homologies are correct, but general appearances, in groups as isolated as the Lagomorpha appear to be, are frequently misleading. A fuller discussion of the homologies is reserved for a later section (pp. 355, 356). All the lower teeth, permanent and deciduous, have an anterior and a posterior root, except $M\bar{3}$, where they appear to be fused.

In $P\bar{3}$, the anterior lobe consists of a buccal and a lingual cusp, each of which has an anterior arm, though that of the buccal cusp is usually the longer. These cusps are probably the metaconid and protoconid, and the anterior arm of the latter may represent the last remnant of the protoconid-paraconid crest. The protoconid has a rounded buccal margin, and the metaconid a distinctly angulate and highly compressed lingual tip. Between the two is a basin, opening broadly at the anterior end of the tooth. This basin is, however, sometimes converted into an extremely ephemeral lake after a small amount of wear (Fig. 81). The posterior margin of this basin is formed by posteriorly directed crests from the protoconid and metaconid, which meet in the center of the tooth at an angle of about ninety degrees, forming a metalophulid II. It is at the apex of this angle that the dentine areas of the trigonid and talonid are first united (compare Figs. 86, 87 and 88). After wear has destroyed its basin, the trigonid is reduced to an oval lobe, surrounded by a narrow band of enamel. Subsequently, the enamel becomes reduced and eventually lost on the lingual side of the tooth. Similar reduction of the enamel is characteristic of all the lower teeth. The trigonid is higher than the talonid, though by no means so much so as is the case in the other lower teeth. As wear proceeds, the cement deposits, which initially covered the entire crown, are rapidly restricted in their distribution, and eventually are preserved only in the hypostriid and mesostriid. The talonid, when unworn (Figs. 74, 84 and 86), consists of a series of low, rounded cusps, rising from the general level of the crown surface, and connected to each other by a series of low ridges. Usually these features are thoroughly masked by a deposit of cement. At the buccal margin is a narrow cusp, reduced almost to a blade in some specimens (see Fig. 86), which is probably the hypoconid. From it diverge two crests, one of which runs antero-mesiad along the margin of the crown, and ending anteriorly, just behind the trigonid, in a large, rounded, blunt cusp, of very uncertain homologies. The posterior crest of the hypoconid extends a short distance along the posterior margin of the crown, before dividing into two crests, which extend, almost parallel to each other, to the lingual margin of the tooth. In entirely unworn teeth (Fig. 86), there is no trace of a cusp at the point of separation of the crests. With slight wear, however (Fig. 84), a small dentine area appears here, which suggests a hypoconulid. The anterior of the two crests from this point extends directly linguad, ending at a large cusp which forms the rounded

lingual side of the tooth, presumably the entoconid. This crest would then be the hypolophulid II. The posterior crest, following the posterior margin of the tooth, would be a posterolophid. There appears to be considerable variation in the talonid basin. In one specimen (A.M.N.H. No. 8052, Fig. 84), the basin is large and quite deep. In another specimen, even less worn (Fig. 86), the basin is almost non-existent, and a clearly marked crest runs antero-posteriorly across it, from the posterior angle of the metalophulid II (which angle is poorly marked in this specimen) to the middle of the hypolophulid II. Variation of this sort, which would be considered of specific or even generic value in brachyodont teeth, is a very common feature in the crown patterns of extremely hypsodont teeth, in which the pattern has not taken part in the increased hypsodonty, and is of no taxonomic significance whatever. In this same category belongs the accessory anterior cuspule on the trigonid which Dice and Dice reported (1935, p. 460 and Pl. XCIII, Fig. 6). With wear, the talonid becomes an irregular enamel ring around a central dentine prism, with four main excrescences, representing the entoconid, hypoconid, hypoconulid and the mesio-buccal cusp, respectively (Fig. 88). At this stage of wear, the two halves of the tooth become connected through the posterior angle of the metalophulid II, the dentine masses soon becoming confluent. At this time the tooth has acquired the fundamentals of the typical palaeolagine pattern, though the talonid still shows numerous irregularities of outline. With increased age, these irregularities are rapidly reduced, a stage soon being reached (Fig. 90) where there are faint irregularities in the enamel outline along the anterior side of the talonid and the posterolophid is still preserved as a distinct fold on the lingual side, though it has disappeared from the buccal side. At this stage, all other traces of the pattern have been lost. It was a tooth in this stage of wear that Walker (1931*b*), as Dice and Dice have already pointed out (1935, pp. 462–463), used as the basis of his genus *Protolagus*, characterized by the possession of three lobes instead of two. This same character, together with the deciduous teeth, was used by Cope (1873*a*) as the basis upon which to found the genus *Tricium*. Later, in describing the milk teeth and the unworn permanent teeth of *Palaeolagus*, Cope recognized that *Tricium* was not valid, stating that "this lobed form of the molars is so different from that of the adult as to have led me to describe it as indicating peculiar species under the name of *Tricium avunculus* and *T. annae*" (1884, p. 877). Thus Cope antedated Walker by fifty years in founding a new genus of rabbits on the unworn teeth of *Palaeolagus*. Further wear results in the elimination of all traces of the posterolophid, leaving only irregularities along the anterior face of the talonid (Fig. 91). From this stage through most of the lifetime of the individual, lakes are entirely absent from the crown. As old age approaches, however, the lingual valley between the talonid and the trigonid is worn away, and eventually the two halves of the tooth are united at the extreme lingual margin, and the outer part of the lingual fold is left as a lake. This is one of the diagnostic differences from *Megalagus*, in which this lake never occurs, and the similar one is very evanescent. Concerning this part of the tooth, Burke states that "In *Palaeolagus haydeni* Leidy the reëntrant corresponding to the median internal reëntrant seen in $P\bar{3}$ of *Palaeolagus turgidus* Cope not only shows marked persistence, . . . but also appears to differ from the same reëntrant of the *turgidus* group in being composed of an inner and an outer portion which are separated by wear, the inner portion being represented by a vertical groove on the internal face of the crown, while the outer part cuts downward into the crown and shows as a pit in an isolated enamel island on

the worn superior surface of the tooth" (Burke, 1934, p. 412). The vertical groove on the internal face is very faint, and soon disappears. This is shortly followed by the lake, and, in extreme old age, the tooth shows the typical pattern of *Megalagus*, and that which Dice used to define the Archaeolaginae (Dice, 1929, p. 343). By this time the enamel has completely disappeared from the lingual side of the tooth, which renders it a simple matter to distinguish between *Palaeolagus* and *Megalagus*, since the latter has attained this pattern long before the enamel is lost. The crown, in unworn teeth, is covered with enamel, in contrast to the condition in *Hypolagus* (Wood, 1937*a*, p. 35), and in agreement with the normal mammalian condition. This difference from *Hypolagus* is merely one indication of the extensive dental evolution that took place in the Leporidae between the Oligocene and the Lower Pliocene. The above description of the changes in tooth pattern with wear agrees in all particulars with that presented by Dice and Dice (1935, pp. 459–461), but due to my good fortune in obtaining a considerable number of specimens with unerupted teeth, I have placed greater emphasis upon the earlier stages of wear, where the pattern is still preserved, than did those authors. For excellent illustrations of the later stages of wear, see their paper (Dice and Dice, 1935, Figs. 14–25).

As in the case of the upper teeth, there is no cement over the crowns of teeth that have not yet erupted beyond the alveolus. The cement is deposited, however, before the actual eruption through the gums. During most of the individual's lifetime, cement was present somewhere on the tooth, disappearing only with advanced old age. The valleys in the talonid and trigonid are filled with cement as long as they exist, and the cement likewise fills the mesostriid and hypostriid. Associated with the absence of cement from the crowns of teeth that have pierced the bone but have not yet passed the gums is the fact that the cement on the sides of the teeth always ends above the level of the alveolus. This indicates that the cement was deposited at or essentially at the level of the gums, at about the same rate as the tooth was growing. There does not appear to be any other plausible explanation for its absence below the level of the alveolus. The deposit of cement is much heavier and more widely distributed on the lower than on the upper teeth.

"The fourth premolar erupts before the third, and its face always shows a small amount of wear at the time when the third deciduous molar is lost" (Dice and Dice, p. 461). $P\overline{4}$ has a pattern similar to that described above for $P\overline{3}$ (Figs. 74 and 84). The trigonid is much higher than the talonid. It consists of the metaconid and protoconid, connected both anteriorly and posteriorly by marginal crests, thus surrounding a central basin. Near the protoconid, and helping to form the anterior side of the tooth, there sometimes is a cusp of entirely unknown origin (Fig. 84). The trigonid basin, unlike that of $P\overline{3}$, does not have an anterior exit, the enamel wall completely closing it in. The basin is, however, almost entirely filled with cement (Figs. 74 and 84). Initially, the trigonid is oval or semilunar, but it later acquires the pinched buccal margin so characteristic of rabbit lower teeth. The trigonid is much wider than the talonid, as in all lower teeth except $P\overline{3}$ (see Tables of Measurements, pp. 319, 323). This talonid consists of the same cusps as in $P\overline{3}$, but the cusps appear to be more rounded and the crests less clearly differentiated from the general surface of the talonid. The tooth figured (Fig. 84) has a surface of very low relief, and the boundaries between the crests and the valleys are very indistinct. The hypolophulid II extends directly across the tooth in an almost straight line. The posterolophid leaves it at right angles for a short distance, and then curves linguad in an abrupt sweep.

As a result, the third lobe is much more distinct from the talonid in this tooth than it is in $P\bar{3}$. There is a strong crest from the entoconid which extends forward to the trigonid. With progressive wear, the two halves of the tooth rapidly become reduced to enamel ovals, though for a while the talonid shows an accessory lobule, due to the presence of the posterolophid. After wear has reached the base of the hypoconulid, so that it no longer shows in the outline of the tooth, an event which happens quite quickly, the teeth have attained what is usually recognized as the typical *Palaeolagus* pattern (Fig. 75). Cement is restricted to the valleys between the talonid and the trigonid. Slight further wear results in the elimination of the enamel from the anterior side of the talonid. At this stage, the two lobes look as if they were about to unite in the same manner as they did in $P\bar{3}$, although actually they do not unite at this time or in this manner. From now on, there is little change in the tooth pattern until late in life. At about the time that the lingual enamel begins to peter out (which happens because the enamel organ stopped depositing enamel on the lingual side before it did so on the other sides, and before the roots began to form), wear lowers the trigonid until it is only slightly higher than the talonid, and shortly brings about their union at the lingual margin, thus resembling such later forms as *Hypolagus* and *Lepus*. This is another progressive leporid character which is merely a senescent *Palaeolagus* character moved up to early life or maturity in the Pliocene to Recent genera. The same is true for the loss of the enamel on the lingual side of the lower teeth and the buccal side of the uppers. Further wear results in the shortening of the external fold, "and in the oldest specimen which we have seen, . . . it extends only about one third of the way across the tooth" (Dice and Dice, 1935, p. 461).

"Both $M\bar{1}$ and $M\bar{2}$ are in position and are very slightly worn at the time of the eruption of $P\bar{4}$" (Dice and Dice, 1935, p. 461). $M\bar{1}$ is similar, both in its pattern and in the changes induced by wear, to $P\bar{4}$. The accessory cusp near the protoconid does not, however, usually appear to be present. In the specimens figured (Figs. 76, 83 and 85), the talonid laps around the posterior V of the trigonid to a much greater extent than has been seen in any specimen of $P\bar{4}$. The crown pattern of the talonid is even more obscured by the reduction in height of the crests and the development of accessory commissures than is the case in $P\bar{4}$. From the figure, it would appear that the talonid basin has been almost entirely obliterated, and that a secondary basin is developing on the buccal margin of the tooth, between the hypoconid and the anterior unnamed cusp. The anterior arm of the entoconid is considerably strengthened. In unworn teeth, there is an entirely distinct third lobe, which is separated completely from the hypolophulid II. Although the primary part of the pattern in this lobe is the crest that was present in the same position in $P\bar{4}$, there is an additional crest forming the hypotenuse of the triangle, the other two sides of which are formed by the angulate posterolophid. With wear, this third lobe is soon attached to the talonid (Fig. 83), and thereafter rapidly disappears (Figs. 74 and 75). The pattern changes with wear in the same manner as in $P\bar{4}$, except that, in early maturity, the enamel is lost from the anterior side of the tooth. In part this may be due to interdental wear (as described by H. E. Wood, 1938, pp. 5–10), but most of this is due to reduction in the deposition of the enamel, since the enamel has thinned over a considerable area where there is no possibility of interdental abrasion, and since the thinning occurs even in the alveolus, where interdental abrasion is out of the question.

$M\bar{2}$ is similar in most respects to $M\bar{1}$, but differs in that the abortion of the pattern

of the talonid has proceeded even farther (Fig. 76), there being no talonid basin at all, and the third lobe is even larger and more complex than it is in $M\overline{1}$ (Fig. 83). The modification of the pattern with wear proceeds in almost exactly the same manner as it does in the anterior teeth. In extreme old age, the lingual fold shows a number of crenulations, not seen at any other stage of wear (Dice and Dice, 1935, Fig. 25).

"The third lower molar . . . erupts at about the same time as $P\overline{3}$" (Dice and Dice, 1935, p. 462). $M\overline{3}$ appears to be, in general, a miniature replica of the other teeth, but it is very much simplified (Figs. 74 and 83). Practically no trace of the trigonid basin is left. The two lobes are clearly visible, each apparently formed of two cusps. The posterolophid is also present, and is both small and simple. It does not take long to bring about the elimination of this last, only a little wear being necessary, since, correlated with the reduced size of this tooth, the pattern-bearing portion of the crown is reduced even farther than in the other cheek teeth. This is probably the reason why Dice and Dice (p. 462) considered that the absence of the posterolophid was the normal condition, and its presence was abnormal. In all specimens which I have seen, in the correct stage of wear, it has, however, been present. No complexities of any sort are visible in the talonid. After a very small amount of wear, the tooth develops a pattern similar to that of the typical *Palaeolagus* $P\overline{3}$ (Fig. 75), except that the buccal valley is very shallow and the lingual valley is deep. But slight additional abrasion is needed entirely to eliminate the buccal valley. Further wear results in the union of the trigonid and talonid at the lingual margin of the tooth, surrounding an ephemeral central lake. Throughout most of its life, $M\overline{3}$ is preserved solely as a single dentine prism with an enamel casing. "In the oldest stages of wear $M\overline{3}$ consists of a single flattened plate with enamel only on its outer edge" (Dice and Dice, 1935, p. 462). Apparently *Mytonolagus* is appreciably more primitive with respect to the reduction of this tooth than is *Palaeolagus*, Burke stating that it is larger than in any of the Oligocene species (1934, p. 413).

The *lower milk teeth*, as in the case of the upper ones, show a very interesting and significant pattern. They do not, however, fit into a series with the permanent premolars, as is the case with the upper milk teeth, but are distinctly more specialized. This is particularly true of $dP\overline{3}$ (Figs. 77 and 85). This tooth has three main lobes and a small accessory one. The central lobe consists of two cusps, from which extend crests converging posteriorly. These cusps appear to be the protoconid and metaconid, homologous with the similar cusps of the permanent teeth. If this interpretation is correct, the single large cusp forming the anterior lobe would be an anteroconid, and would represent an enlargement of the anterior wall of the trigonid of the permanent teeth. This is quite possibly the key to the evolution of $P\overline{3}$ of the Leporinae. The deep valley and fossa between the anterior two lobes of $dP\overline{3}$ would then merely be an immensely hypertrophied trigonid basin. With wear, this part of the tooth becomes two dentine prisms, clearly and distinctly separated (Fig. 85). Next, the two lobes unite on the buccal side, in the same manner as the talonid and trigonid of the molars do, except that the union occurs on the opposite side of the tooth. Eventually, the buccal end of the lingual fold is isolated as a pit. At this time, the pattern is very suggestive of that of $P\overline{3}$ of the Leporinae (Dice and Dice, Figs. 9–11). This lake soon disappears. The pattern of the talonid is rather similar to that of the corresponding part of the permanent teeth, and shows no striking differences. The talonid basin is almost completely eliminated by being broken up into a series of small

basins. With wear, the talonid becomes a single dentine surface, from which the large posterolophid is given off as a semi-distinct lobule. Later this too is lost. The talonid and trigonid rapidly unite, first in the middle of the tooth as they do in $P\bar{3}$, and very soon afterward on the buccal side, forming a lake in a manner analogous to that by which it is formed in the permanent tooth. "In very late stages of wear . . . $DP\bar{3}$ has entirely lost the internal reëntrant angle, but the external reëntrant angle still persists. In this very late stage of wear enamel occurs only on the outer border of the tooth and in the reëntrant angle. The roots of the anterior deciduous molar . . . penetrate deeply into the jaw, almost coming into contact with the root of the incisor. When the crown of this deciduous molar has disappeared the roots remain in place for a short time" (Dice and Dice, p. 457).

The pattern of $dP\bar{4}$ is very much more like that of the permanent teeth (Figs. 77 and 85) than is that of $dP\bar{3}$. In the unworn tooth, however, the posterolophid is much more of a distinct lobe than is the case in any of the permanent teeth. In this tooth, also, the talonid basin is reduced practically to the vanishing point. It agrees with $dP\bar{3}$ and differs from the permanent teeth in that the trigonid and talonid unite, upon wear, on the buccal side first, instead of on the lingual side. "At this stage the enamel of the two pillars comes into very close contact in the middle of the tooth and gives an appearance almost of fusion, but in none of the specimens which we have examined is there an enamel connection at this place. In a late stage of wear . . . the large external reëntrant angle of $DP\bar{4}$ is much reduced and extends only about halfway across the tooth. In this stage of wear enamel is present only on the reëntrant angle and on the outer surface of the tooth" (Dice and Dice, p. 458). Burke states that, in *Mytonolagus*, "antero-internally a notch appears on the anterior lobe of this tooth" (1934, p. 414). I have seen no trace of this in any of the White River forms.

The size of the teeth in *Palaeolagus* is as much an age character as it is indicative of anything else. The measurements given below (pp. 318–323) vary within wide limits, depending on the age of the individual measured. As no particular measurements appear to have more significance than others, those given in the tables are the diameters of the wear surfaces. Those taken at any other point would vary equally widely. The teeth increase in transverse diameter very notably, and decrease correspondingly in antero-posterior diameter until extreme old age, when the transverse diameter likewise decreases.

The occlusion of the cheek teeth of *Palaeolagus* is quite interesting. A characteristic feature of the lower teeth is that the trigonids are very much higher than the talonids, and that the surface of the talonid of one tooth forms a continuous surface with the trigonid of the tooth behind it. In spite of this, the trigonid of each tooth rises as high above the level of the mandible as does that of the tooth in front of it. This is because the teeth are at an angle to the mandible. Since the wear surfaces cut the teeth at right angles to their semi-vertical axes, they too are at an angle to the jaw. In the lower jaw, the wear surfaces face forward and upward, and in the upper teeth they face downward and backward. Each upper tooth, then, occludes, as would be expected, with the talonid of the corresponding lower tooth and the trigonid of the one behind it. Antero-posterior motion is completely eliminated by the high ridge of the trigonid rising in front of each wear surface in the lower teeth, and by the corresponding ridge formed by the anterior face of each of the upper teeth at the posterior margin of each wear surface in the upper jaw. There is, however,

absolutely nothing to restrict the free transverse movement of the jaws, so that mastication in the rabbit is performed exclusively by this type of motion.

The *vertebral column* consists of seven cervical, about twelve thoracic, about seven lumbar vertebrae, one sacral, two pseudosacrals and an unknown number of caudals, probably not very large. The only specimen with which I am familiar that preserves any appreciable part of the vertebral column is Univ. Michigan No. 14,317, and it has been deemed inadvisable to make any attempt to prepare the vertebrae of this specimen in any detail, since they are, to a large extent, covered by parts of the skull or of the appendicular skeleton. In *Lepus*, the vertebral formula, as far as is known, agrees with that of *Palaeolagus*. In *Ochotona*, on the other hand, the thoracic vertebrae have been increased to sixteen, and the lumbars reduced to six. The cervical series of the fossil is arched as it is in the skeleton of the living forms. The specimen of *Palaeolagus* cannot be prepared sufficiently to determine whether the bones are articulated in this pose, but nevertheless it suggests that the fossil held its head in a position similar to that in which the modern rabbits hold theirs, although it is also quite likely that the bending of the neck in this specimen is due to contraction of the cervical tendons after death. In the restoration (Fig. 78*a*), this explanation has been accepted, and the animal restored with the head more nearly a prolongation of the axis of the vertebral column than it is in the living leporids. The spines of the thoracic vertebrae are long, as in the modern rabbits. This indicates strong neck muscles, an initial stage in the leaping adaptation. In the lumbar vertebrae, the transverse processes are much shorter than in the modern forms, and the zygapophyses are not as high above the centrum as in Recent leporids. The interlocking of the lumbars by the backward growth of the anapophyses is just beginning in *Palaeolagus*, suggesting the strengthening of the skeleton in the early adaptations to leaping. Since, however, this same process is taking place in *Ochotona*, it must be considered a primitive lagomorph character, homologous to the strengthening of the vertebral column in the African Hero Shrew, rather than something developed in correlation with the strengthening of the vertebral column for leaping.

There is a single *sacral*, as in modern forms, and two *pseudosacrals*. The ilio-sacral articulation consists of two parts, arranged in a U, with the opening anterad. The dorsal part has the same shape as the ventral and is nearly as long, in *Palaeolagus*, instead of being round and short, as in *Lepus*. *Ochotona* is intermediate between the other two in this respect. The two arms of the U are nearly parallel, instead of diverging sharply as in *Lepus*. This makes the union of the sacrum and pelvis less firm than in the jack-rabbit. The facet does not extend appreciably below the ventral margin of the centrum of the sacrum, as it does in *Lepus*. Nor are the facets as much inclined away from the vertical as they are in that form. These would seem to be specializations in *Lepus* for getting the legs under the animal in order to be better able to leap. The pseudosacrals are of more nearly the same width as the sacral than is the case in the living forms, indicating a longer and stronger tail even than in *Lepus*. The first pseudosacral is as firmly fused with the sacrum as it is in *Lepus*. Ventrally, there is no sign of the two ridges leading posterad from the anterior end of the sacral centrum in *Lepus*, but merely a single median ridge, larger than the median ridge of *Lepus*. This would seem to mean that the *flexor caudae* is much stronger in *Lepus* than it was in *Palaeolagus*. The sides of the first pseudosacral tend to become parallel at its posterior end, again indicating a wider and heavier tail than

in any modern lagomorphs. Nothing is known of the caudal series in *Palaeolagus*. In the restoration (Fig. 78*a*) the tail has been restored from that of living rabbits, but has been made slightly longer.

The dorsal portions of the *ribs* are very much more arched in *Palaeolagus* than are those of *Lepus* and *Sylvilagus* or *Ochotona*. The angle is farther from the vertebral column, in proportion to the size of the animal, than in *Lepus* or *Sylvilagus*. In all forms, however, the angle is very high on the bone, being level with the centra, and in all it is very pronounced. The ventral part of the shaft hangs almost as straight down as in the Recent forms. The thorax of *Palaeolagus* must therefore have been more capacious than that of Recent lagomorphs.

The *manubrium* is in general similar to that of *Lepus* and *Sylvilagus*, but is much shorter (Pl. XXXVI, Fig. 3). The anterior process, in particular, is very much shorter than in the Recent genera, resembling that of the pika in this respect. The details of the bone are more like those in *Lepus* and *Sylvilagus*. The lateral margins are deep fossae, extending back as far as the attachment of the first costal cartilage. This latter, incidentally, appears to have united with the manubrium at right angles instead of obliquely as in *Lepus* and *Sylvilagus*, suggesting a wider thorax. The space between the first and second costal cartilages was proportionately shorter than in *Lepus* and *Sylvilagus*. The changes in the bone would seem to indicate great strengthening of the sternomastoid in Recent leporids, perhaps correlated with ability to hold the head steady during leaping.

The *scapula* is about twice as high as it is broad in *Lepus*, whereas in *Palaeolagus* it is only half again as high as broad, being very like *Ochotona* in this character. Dice (1933, p. 305) states that it "is shorter and broader proportionately in the fossil than in any other known leporid." The spine follows almost the midline of the bone, instead of being only a third of the way back from the anterior margin, as in *Lepus* and *Ochotona*. The postero-dorsal angle is rounded instead of being angular as in *Lepus*. In *Ochotona*, it is even more acutely angulate than it is in *Lepus*. The neck of the scapula is quite short in *Palaeolagus*, instead of being very elongate as in *Lepus*. This suggests that the animal was not as good a runner as is the modern hare. Since, however, *Ochotona* and *Lepus* are almost identical in this respect, the significance of this character is uncertain. The cranial angle is rounded and extends far forward, as in *Ochotona*, but the supraspinous fossa is very much larger than in that form. In lagomorph evolution, there appears to have been a progressive decrease of the *supraspinatus*, while the *infraspinatus* has remained the same size. This would suggest that the fore limb was more muscular, and therefore presumably of greater use in locomotion, in *Palaeolagus* than in the living lagomorphs. The coracoid process does not seem to have been as large as that either in *Lepus* or in *Ochotona*. The long piece of bone which Dice (1933, p. 305) interprets as "probably the metacromion," does not appear to me to be a part of the scapula, but if it should prove to be the metacromion, I believe that it must have been rotated about ninety degrees from its proper position, which would account for Dice's belief that "compared with modern leporids, this metacromion is remarkably long for the size of the scapula" (op. cit., p. 305).

The *humerus* is much more primitive than is that of *Lepus*. The muscle attachments in the proximal half are more marked than in Recent forms, and the distal end is much wider and generally seems more primitive. The deltoid crest extends 19 mm. from the head as opposed to 27 mm. in *Lepus*. The proximal part of the insertion area of the

*deltoideus* is wide, as in *Lepus*, but it tapers gently distad, as in *Ochotona*, instead of narrowing abruptly about at its middle. In *Lepus*, the wide proximal part is changed to the narrow distal part by a line almost at right angles to the long axis of the bone. This difference in the insertion area suggests a much shorter insertion and a more direct pull, and hence greater speed though less power, for the deltoid in *Lepus* than in *Palaeolagus*. *Palaeolagus* resembles *Hypolagus* (Wood, 1937*a*, Fig. 16) in this respect. The bicipital groove is quite shallow, being much more like that of *Hypolagus* and *Ochotona* than like that of *Lepus* in this respect. The head is less globular and more triangular than is that of *Lepus*, and, in lateral view, does not overhang the shaft as much as in *Lepus* and *Ochotona*. The supinator crest is distinctly expanded, as opposed to the condition in *Lepus*, where it is almost non-existent, or the pika, where it is very small. The supratrochlear fenestra, so characteristic of lagomorphs in general, is well developed. There is a large entepicondylar foramen, absent in all post-Oligocene lagomorphs with which this form has been compared. The keels of the articular surface, which are so pronounced in Recent leporids, are entirely absent, being represented only by rounded ridges, as in *Ochotona* and in general among primitive mammals. The humerus, then, is that of a generalized primitive mammal, lacking most of the striking leporid characters. It is also more primitive than the humerus of the pika. From the appearance of the distal end of this bone in Univ. Michigan No. 14,317, in which it is very well preserved, *Palaeolagus* must have possessed free pronation and supination. The distal end of the humerus, in fact, does not resemble that of *Lepus* at all, and resembles that of *Ochotona* only slightly. This humerus agrees in all points with that figured by Cope (1885, Pl. 66, Figs. 16 and 16*a*). Cope's figures, however, do not show the supinator crest as clearly as it can be seen in the University of Michigan specimen (Pl. XXXVI, Figs. 2, 2*a*). The entepicondyle is smaller and the ectepicondyle larger than in *Hypolagus* (Wood, 1937*a*, p. 37). Cope's figures show the weakness of the intertrochlear ridges. Burke, in his discussion of *Mytonolagus* (1934, p. 414), says: "The skeletal material . . . indicates an animal of somewhat lighter frame than *Palaeolagus haydeni* Leidy. The head of the humerus is less globular than in the latter species, but stands higher than the greater tuberosity. Distally the entepicondylar foramen and the general proportions appear to be much as in *Palaeolagus haydeni* Leidy, but the radial articular surface is less convex." This shows that the loss of the power of pronation and supination, and the increase of the antero-posterior motion of the elbow joint, which characterizes the modern cursorial leporids and to a lesser degree the ochotonids, was taking place to an appreciable degree between the Uinta *Mytonolagus* and the White River *Palaeolagus*. Although *Palaeolagus* was still definitely not saltatorial, and must have been unable to seek safety in sustained flight, it had started to evolve in the direction leading toward a saltatorial habitus, and was farther advanced in this direction than was *Mytonolagus*.

In *Lepus*, the olecranon and the *radius* close in on the distal end of the humerus in the same manner that the pre- and post-glenoid processes close in on the mandibular condyle in the Mustelidae, giving a joint that can not be disarticulated without separating the radius and ulna, or breaking the process on the head of the radius. This is obviously a high specialization toward cursorial locomotion, and is suggestive of the conditions in the higher ungulates. There is no trace of this close locking to be found in *Palaeolagus*, and but little in *Ochotona*. In *Palaeolagus*, the head of the radius is oval, about the same shape as that of *Ochotona*. It is much more elongate and proportionately narrower than

in *Lepus*. Moreover, the head does not show the deep groove that is found in the modern genera, correlated with the lack of keels on the humerus of *Palaeolagus*. Neither is there any trace of the high peripheral ridges which surround the head of the modern forms. The whole articular surface is nearly flat. The rear surface, articulating with the ulna, is flatter than in *Lepus*, and about as flat as in *Ochotona*. The distal ends are similar in *Palaeolagus* and *Ochotona* except that in the fossil this part of the bone is wider and narrower than in *Ochotona*. The keels articulating with the carpus are weaker in both of these forms than in *Lepus*, where they are strongly marked. The proximal half of the radius is free from the ulna, instead of the two bones being closely appressed throughout as in *Lepus* and *Ochotona*. The radius is much more nearly straight in *Palaeolagus* than in *Lepus* or *Ochotona*. Dice (1933, p. 306) points out that in *Palaeolagus* the ulna and radius are of equal thickness, whereas in *Lepus* the ulna is the more slender. This, of course, is the same progressive modification that has taken place in the ungulates, where the cursorial adaptation has led to the virtual elimination of all parts of the ulna except the olecranon. *Ochotona* agrees with *Palaeolagus* in this lack of reduction of the shaft of the ulna, since it too has not begun to develop cursorial adaptations. Dice states that there is a tendency for the two bones to fuse in *Lepus*, a highly advanced character and again paralleling the ungulates. This was not noted in any of the material available to me for comparison. Whether this is a character of some species of *Lepus*, or whether it is an individual variation, I am unable to say.

The *ulna*, like the radius, is very much straighter in the fossil than in the Recent genera. The head of the ulna is strikingly different from that of *Lepus*, and is very much more primitive. The keel below the semilunar notch is much smaller than in *Lepus*, indicating that there are much greater potentialities for transverse and rotational movement than is the case in *Lepus*. The olecranon is nearly a direct continuation of the shaft in *Lepus*, but is rotated mesially in *Palaeolagus*, a primitive character which is also present to a slight degree in the pika. The groove for the tendon of the *triceps* is shallower than in *Lepus*, but deeper than in *Ochotona*. The fossa from which the *flexor carpi ulnaris* arises is broader than in *Lepus*, but not so deeply incised. The distal end of the ulna is very different from that of *Lepus*, ending in a broad articulation with the carpus, as in *Ochotona*, instead of tapering to a thin styloid process as in *Lepus* and *Sylvilagus*. Neither is there any trace of the globular facet at the extreme tip of the shaft, found in *Lepus*. This points to the same conclusion as does the evidence from the other end of the bone—namely that the animal was much less limited to antero-posterior movements of both wrist and elbow than is *Lepus*, but was able to pronate and supinate freely, and to move the forearm freely in a horizontal direction as well as to rotate the wrist about the forearm. In other words, *Palaeolagus* was still a scampering form, with only a few foreshadowings of the initial stages of saltatorial adaptations. The animal was undoubtedly able to use its hands to pick up and hold its food in the same manner as do the rats and squirrels.

The *carpus* of *Palaeolagus* is still entirely unknown. A small portion of the manus is, however, preserved as part of Univ. Michigan No. 14,317. The best preserved of these fragments are metacarpals II and III. The former is proportionately as long as, but more slender than, the same bone in *Lepus*. This appears to have been the longest of the metacarpals. The facets on the proximal end show that its articulations with the carpus were like those of *Lepus*, suggesting that at least the distal row of carpals were similar in

the two forms. Metacarpal III was long and slender, resembling its neighbor, though it is not quite as long. Its head articulated beneath the overhanging head of metacarpal II as in Recent forms, but the two bones were not so closely appressed in the fossil, there being no trace of the facets on their adjoining surfaces which are so clearly visible in *Lepus*. The manus appears to have been very much more like that of *Ochotona* than like that of *Lepus*, both being spreading hands, adapted for holding food, rather than being primarily used in locomotion. The manus of *Palaeolagus* was like that of *Lepus*, however, in the near equality of size of these two metacarpals, tending to strengthen the inner side of the hand.

In general outline, the *pelvis* appears to have been rather similar to that of other leporids, such as *Lepus*, *Sylvilagus*, and, as far as is known, *Hypolagus*, but to have been quite different from that of *Ochotona*. On closer study, however, there are a considerable number of differences detectable between the pelves of *Palaeolagus* and the later leporids, best exemplified in the ilium. The ilium is strikingly trihedral in *Palaeolagus*, with clearly marked superior and inferior gluteal fossae, separated by a sharp crest, as pointed out by Dice (1933, p. 306). The two fossae are nearly at right angles to each other. In *Hypolagus*, the two fossae are still present, but the ridge between them is lower, and they are no longer so clearly at right angles to each other (Wood, 1937*a*, Fig. 17). In *Sylvilagus* and *Lepus*, this reduction of the crest and the rotation of the two fossae continues until, in the latter form, the crest is merely a faint dome and the two fossae are almost co-planar. This evolutionary sequence is in striking contrast to the developments in *Ochotona*, where the angle between the two planes is reduced to about seventy-five or eighty degrees, and the superior fossa has grown while the inferior one has decreased almost to the vanishing point. The size of these fossae in the leporids is correlated with the strength of the adductor muscles of the thigh, so important in leaping. The small size of the same muscles in *Ochotona*, and their fusion with each other (Camp and Borell, 1937, p. 320), is undoubtedly correlated with the absence of the leaping adaptation in that form. The tubercle of the ilium is extremely high, forming the summit of the high narrow ridge which forms the ventral border of the inferior gluteal fossa and which extends nearly to the acetabulum. The tubercle is not as near the acetabulum as in *Lepus*, *Sylvilagus* and *Hypolagus*, but is in about the same position as in *Ochotona*. In none of these last genera does it have any connection with the ventral border of the gluteal fossa, being continued by a faint ridge into the middle of the fossa in the leporids, and by an equally faint ridge to the crest between the two fossae in *Ochotona*. In *Palaeolagus*, only the tip of the tubercle was used for the attachment of the ligament, whereas in all the other leporids the ligament spread onto the dorsal surface of the tubercle, resulting in a greater strength for the attachment. *Ochotona* agrees with *Palaeolagus* in this. Correlated with this change, the tubercle in Recent leporids no longer rests on a high pinnacle as in *Palaeolagus*, but becomes a knob on the surface of the bone in *Sylvilagus* and *Lepus*. In *Ochotona* and *Hypolagus*, it is in an intermediate stage. This lowering of the tubercle undoubtedly increases the strength of the origin of the *rectus femoris* and hence the leaping power of the animal. In the series, *Palaeolagus*, *Hypolagus*, *Sylvilagus* and *Lepus*, there is progressive decrease in the height of the tubercle and of its distinctness as a process separate from the rest of the bone, together with a progressive increase in the size of the area for the origin of the muscle. There appears to have been a much smaller amount of flare to the crest of the ilium in *Palaeolagus*

than in *Lepus*, and a considerably smaller amount than in *Hypolagus* and *Sylvilagus*. This would appear to be correlated with the smaller size of the fossil genus than any of the later forms. In support of this conclusion, the ilium of the pika has even less flare than that of *Palaeolagus*. There is no evidence that there was any trace in *Palaeolagus* of the hook which is present at the anterior end of the ilium of *Ochotona*. The ilium is longer proportionately in the fossil than in Recent leporids, but is very much shorter than in the pika, showing that the angle at which the *rectus femoris anterior* and *tensor fasciae latae* pulled in the fossil was less than in the pika and greater than in Recent leporids, indicating a speed intermediate between that of those two groups (Camp and Borell, 1937, p. 318). The notch marking the posterior end of the sacral articulation is opposite the anterior end of the tubercle, but is sharper than in *Hypolagus*, *Sylvilagus*, *Lepus* and *Ochotona*. The acetabulum is like that in other leporids, but differs from that of *Ochotona* in that it is almost closed posteriorly. In at least some specimens of *Sylvilagus*, the acetabulum is entirely closed. No difference at all was noted between *Palaeolagus* and *Hypolagus* in the characters of the acetabulum. In all the forms studied, the main axis of the pelvis continues directly from the ilium through the ischium. Although the posterior tip of the ischium is broken off in University of Michigan No. 14,317, it appears to have had somewhat of a flare, suggesting the initial stages in the process seen in *Sylvilagus* and *Lepus*, where this part of the bone is widened into a broad plate, and extended far behind the obturator foramen. This, of course, is to supply sufficient area of origin for the great extensors of the thigh, which are the primary muscles involved in saltation. The apparent expansion of this region in *Palaeolagus*, and the suggestion of a small crest at the dorsal margin of the bone, indicate that this genus was in the initial stages of acquiring the leaping ability. The absence of such a crest or of any expansion of the ischium above the axis of the bone in the pika is an indication of the weakness of the flexors in that form. In all the forms that have been studied, "the muscles that originate on the posterior portion of the innominate bone . . . pull at about the same angle" (Camp and Borell, 1937, p. 318). The obturator foramen is longer and proportionately of less vertical diameter in *Palaeolagus* than in *Lepus* or *Sylvilagus*, approaching more nearly to the latter in this respect. It is quite different from that of *Ochotona*, which is egg-shaped, with the large end posterior. This is correlated with the very short *symphysis pubis* in the pika, due to the rotation of the pubis backward from the acetabulum until it forms an angle of only thirty degrees with the ischium, as contrasted with the angle of sixty degrees in *Palaeolagus* and *Hypolagus* and seventy degrees in *Sylvilagus* and *Lepus*. The backward rotation of the pubis in *Ochotona* has resulted in the reduction of the anterior part of the obturator foramen. The pelves are fused along the *symphysis pubis*, which is about as long in *Palaeolagus* as in the other leporids. "In *Ochotona*, the two halves of the pelvic girdle are not fused and the short inferior rami of the ischium and pubis are joined by a thick ligament. . . . The fusion of the two halves of the pelvic girdle . . . produces a stronger and more rigid girdle than the type found in *Ochotona*, and increases the support of the longer limbs and heavier muscles of *Lepus*" (Camp and Borell, 1937, p. 317). *Palaeolagus* thus had the potentialities, in the pelvis, for development into a leaping form.

In no specimen of *Palaeolagus* that I have seen is the entire *femur* preserved. By piecing together material from various specimens, it is possible to get a pretty good idea of the characteristics of the bone. The femur of *Palaeolagus* is straighter than that of modern

leporids, and is nearly as straight as that of *Ochotona*. Two specimens of the proximal end of the femur are included in A.M.N.H. No. 9655-57. These are enough like those of *Lepus* and *Sylvilagus* to warrant their being considered as belonging to *Palaeolagus* in spite of the considerable differences of the fossil from the Recent genera. The width of the proximal end is much greater in the Recent forms. In all lagomorphs, the groove between the head and the greater trochanter is small, the neck is almost non-existent, and the head is set on the proximal side of the neck, at right angles to the long axis of the shaft, instead of being at right angles to the neck, as is more usual among mammals in general. This means that the shaft of the femur is always at an angle of thirty degrees with the vertical plane of the ilio-sacral articulation, approximately as in *Lepus* and *Sylvilagus*. The head and the greater trochanter are, however, of about the same height, as in *Ochotona*, instead of the trochanter overhanging the head as is the case in the Recent leporids. The *fossa ligamenti teris* is entirely isolated. The posterior side of the greater trochanter has grown mesiad in the Recent forms, changing the trochanteric fossa from a simple fossa to an almost enclosed pocket. The proximal end of the trochanter in *Palaeolagus* appears to have been converted to the anterior side in the Recent forms by the upgrowth of the lateral and posterior parts of the trochanter. This suggests that the *glutaeus medius* and *minimus* are larger in the Recent leporids and that this change in the muscles has induced the modification of the trochanter. It is quite possible that these muscles were incompletely separated in *Palaeolagus* as in *Ochotona* (Camp and Borell, 1937, p. 320). The *gemelli*, *obturator externus* and *obturator internus* were probably inserted by weaker tendons than in Recent lagomorphs, since the trochanteric fossa is not so deep in the fossil. If the tendons were weaker, the muscles were probably likewise weaker. The lesser trochanter is even larger in *Palaeolagus* than in the living forms. The difference in the proximal end of the bone between the Oligocene and Recent forms is largely due to the change in the position of the third trochanter, which is distad of the lesser trochanter in *Palaeolagus*, whereas in the Recent forms, even including the pika, it has moved proximad until it is opposite the lesser trochanter. This indicates that in the modern genera, the *glutaeus maximus* and *quadratus femoris* have a shorter pull and therefore act much more quickly than they did in the fossil. This is an expectable evolutionary modification, as those animals which could move the fastest would be the most likely to survive. The change in the position of the third trochanter and the widening of the bone across the head and greater trochanter account for the differences between *Palaeolagus* and the Recent forms in the proximal end of the bone. The posterior side of the femur is flattened in *Palaeolagus* as in *Lepus*, *Sylvilagus* and *Ochotona*. In all forms, the patellar groove extends far up the anterior side of the bone, which appears to be an ordinal character of the Lagomorpha. No significant differences in the distal ends of the bones were encountered among any of the lagomorphs.

The *tibia* and *fibula* differ but little from those of Recent lagomorphs. The distal portions of the two bones are entirely fused, and the relationships of their proximal portions are similar, throughout the order. In fact, there is very little variation even in the percentage of fusion of the two bones among any of the lagomorphs studied, although the two bones are fused for a slightly smaller part of their length in *Palaeolagus* than in the other members of the order in which the tibiofibula is known. This extremely small progress in increasing the fusion of these bones since the Oligocene indicates how slow lagomorph evolution has been even in those parts of the skeleton where evolutionary change has been the

most rapid. The situation in *Palaeolagus* is appreciably more primitive than in the Pliocene and Recent lagomorphs, but rather little so. Burke (1934, p. 414) has pointed out that in *Mytonolagus* the tibia and fibula are fused, but his material was too fragmentary to permit the taking of any measurements. He also states that the proximal end of the bones is like that in *Palaeolagus*. The fibula appears to have been distinctly heavier in *Palaeolagus* than in modern leporids, although it is broken in all specimens that I have seen. Just above the point of fusion of the two bones, the fibula was apparently about a third as wide as the tibia, though proportionately much more slender. The cnemial crest is much more pronounced than in *Sylvilagus* and very much more so than in *Hypolagus* (Hall, 1930, Fig. 22), and rises to a prominent point at its distal end, as in *Lepus*, but less pronounced than in *Ochotona*. The patellar facet is lower than in *Hypolagus* and much lower than in *Sylvilagus*. The cnemial crest has much more mesial overhang than in *Sylvilagus*, *Lepus* or *Ochotona*, perhaps indicating a stronger insertion of the *gracilis*. The fused portion of the tibiofibula is not of uniform width as in *Sylvilagus* and *Hypolagus*, but tapers from the point of fusion nearly to the distal end. The proximal portion of the fibula is likewise of variable width, the only suggestion of this that was seen in Recent forms being in *Ochotona*, where there were also variations from place to place in the width of the fibula. The head of the tibia has the same shape as in *Sylvilagus*, but the facets for the condyles of the femur are very poorly developed, not being as clear even as they would appear to be in *Mytonolagus* (Burke, 1934, Pl. L, Fig. 9). The facets resemble those of *Ochotona* very much. This suggests quite definitely that this joint in *Palaeolagus* was a much less perfect hinge than in the modern leporids, and that the powerful spring of the hind legs, which serves as the principal means of locomotion in the living forms, had not yet been developed. The mesial facet does not overhang so much to the rear as in *Sylvilagus*, being more like that of *Hypolagus* in this respect. The distal end of the tibiofibula of *Palaeolagus* shows the same characteristically low keels as are seen in the other articular surfaces of this animal. The fibular epicondyle is shorter and more hooked than in *Sylvilagus* and *Lepus*. The calcaneal articulation is narrower than in those forms, though most like that of *Sylvilagus*, and is crescentic rather than oval. The groove for the mesial keel of the astragalus crosses the entire bone, instead of being separated from the anterior face of the tibiofibula by a ridge, as in *Sylvilagus* and *Lepus*. The fossa for the lateral keel is very much fainter than in *Sylvilagus*, and the fossae are more nearly abreast of each other than in the Recent genera. The anterior face of the bone shows a very marked groove between the tibia and fibula, which is entirely lacking in *Sylvilagus* and *Lepus*, and only a trace of which is present in *Ochotona*. This indicates an approach toward the time when the two bones were entirely separate. From the subsequent rate of evolution of the tibia and fibula, one might hazard a guess that the two bones were separate in the Upper Paleocene but began to fuse by the Lower Eocene. The distal end of the tibiofibula curves forward instead of being a direct continuation of the shaft as in *Lepus*, in this agreeing with the conditions in *Sylvilagus* and *Ochotona*. There is no difference in the arrangement of the parts of the distal end between *Palaeolagus* and the Recent forms. The chief difference in this part of the fossil from the corresponding parts of the living genera is that the bone in the former is much more slender and the facets are much less sharply marked than in Recent forms. The median malleolus is at the distal end of the bone instead of being slightly proximad of the end as is the case in *Lepus*. This bone, then, adds another to the items showing that *Palaeolagus* had poorly

developed keels at its joints, and hence that it was much less adapted for rapid running than are the modern leporids. As far as can be told from the tibia and fibula, the animal had habits of locomotion similar to those of the pikas today.

In spite of all the material of *Palaeolagus* that is available for study, I have nowhere seen a complete foot, or even a complete tarsus, of the animal. A very considerable number of specimens have, however, been encountered which contain one or more of the tarsals, and it is upon a study of all of these that the following description is based. In general appearance, all the tarsals resemble those of Recent forms, though naturally there are many minor differences.

The *calcaneum* particularly is like that of living leporids. However, the tuber calcis is less elongate, proportionately, than in *Lepus* and *Hypolagus*, and about the same relative length as in *Sylvilagus* and *Ochotona*. This indicates a weaker leverage for the *gastrocnemius* than exists in *Lepus* and *Hypolagus*. The tuber is not grooved for the tendon of Achilles in *Palaeolagus*, whereas it is quite markedly grooved in the two Recent leporids, and slightly so in *Hypolagus*. This is another indication of the inefficiency of the *gastrocnemius* in *Palaeolagus*. There is a median process of the tuber in the Recent leporids, on the median side of the groove, barely suggested in the fossil. This appears to mark the insertion of the *soleus*, and suggests that that muscle also had a weaker insertion, and hence was presumably weaker in general, in *Palaeolagus* than in the other lagomorphs. Just below the keel, on the median side, there is a rugosity in all forms, for the origin of the *flexor digitorum*. This is much heavier in *Lepus* than in the other genera. The facet for the fibula is very nearly identical in all four forms, differing in *Palaeolagus* from the others in that it has a more abrupt distal termination. The ectal facet in *Palaeolagus* is broadly oval and convex, differing markedly from those of *Lepus* and *Sylvilagus* by having no sign of the strong crest dividing it into two facets. In fact, in *Palaeolagus* it almost looks as if there might have been slight movement between the astragalus and the calcaneum, which definitely could not occur in the living genera. Nor could such motion have occurred in *Megalagus* (see below, p. 338). The ental facet is of nearly the same shape in all three forms. In *Palaeolagus*, however, the process supporting this facet is distinctly more prominent than in the other two genera. Just below the keel, on the median side, there is a foramen in all four forms. In *Palaeolagus*, it is just mesiad of the cuboid facet, and below the neck of the astragalus. It is slightly further distad in *Lepus* than in *Palaeolagus*, and larger proportionately in the latter. It is much larger in *Palaeolagus* than in *Sylvilagus*. The canal, of which this foramen is the distal orifice, has a different angle in *Palaeolagus* from that in the Recent genera, passing almost straight through the bone in *Palaeolagus*, instead of being straight for part of the distance and then bending sharply upward as in *Sylvilagus* and *Lepus*. The distal end of the astragalus articulated with the side of the distal end of the calcaneum for a short distance. This articulation takes place via a slightly raised process of the calcaneum in *Palaeolagus*, quite different from the sharply accentuated knob in the Recent genera. There is only a faint trace of the interlocking of these bones seen in *Megalagus*. The upper surface of the calcaneum, distad of the trochleae, is at an angle of about one hundred and twenty degrees with the side facing the astragalus, instead of being at an angle of ninety degrees, as it is in the living leporids. In all genera, the upper surface of the distal part of the calcaneum is broad and nearly flat, with a few minor rugosities, and expands slightly distad. The lateral surface is at an angle of about

ninety degrees with this in *Sylvilagus* and *Lepus*, but only about sixty degress in *Palaeolagus*, in which form it slopes rapidly mesiad toward the plantar side of the bone. The cuboid facet is quite different in shape in *Palaeolagus* from that in *Sylvilagus* and *Lepus*, in which genera it is nearly of identical patterns. In the Recent genera, the main facet is L-shaped, with a long, horizontal upper member and a descending member on the lateral side. In *Palaeolagus*, however, this is a single subrectangular surface, proportionately as high, dorso-ventrally, as the lateral wing of the L in the other genera. In this it agrees exactly with *Ochotona*. In all forms there is another, plantar, facet, for articulation with the plantar process of the cuboid. This is farther distad in *Palaeolagus* than in the other two genera. The part of the cuboid facets on the distal end of the calcaneum of *Palaeolagus* are essentially parts of a single plane surface, as in *Ochotona*, instead of being a curved surface as in *Sylvilagus* and *Lepus*. This indicates a less firm union of the foot bones in the fossil genus, the same story that was conveyed by the ectal facet. This means that the animal was much more primitive in the structure of the pes than are the Recent genera, and was nowhere near as well adapted to a leaping mode of progression. In fact, it was probably not a leaping animal at all, but a scamperer like the modern rats and mice.

The *astragalus* of *Palaeolagus* has the same general shape as that of *Lepus*, but the distal end diverges more from the axis of the keels than in *Lepus*, though less than in *Hypolagus*. In *Lepus*, the axis of the distal end is almost a continuation of the line of the keels, whereas in *Palaeolagus* it is curved medially. This results in a shortening of the astragalus, and hence a shorter tarsus, less adapted for leaping, and therefore more primitive. The keels are straighter in *Palaeolagus*, with a less perfect pulley-like surface. The medial keel is less well developed in *Palaeolagus* than in *Lepus* and *Sylvilagus*, but is very similar to that of *Hypolagus*. The facet for the navicular is very similar in *Palaeolagus* to its condition in modern forms. The tibial keel is clearly shown, extending onto the plantar surface, in Recent leporids and *Hypolagus*, but is barely discernible from this aspect in *Palaeolagus* and *Ochotona*, which indicates a lesser amount of extension of the pes in these last genera. The ental facet does not narrow proximally as sharply as in *Hypolagus* (Wood, 1937*a*, Fig. 18a) or in the Recent leporids. The groove into which the calcaneum fits, especially in the vicinity of the ectal facet, is much more shallow in *Palaeolagus* than in the other genera. In part this is due to the ventral extension of the keels, in part to a deepening of the groove. At any rate, it makes a much more perfect lock in *Lepus* than in *Palaeolagus*. The remainder of the bone appears to be similar in all forms.

The *cuboid* is not very similar to that of Recent leporids. The facet for the calcaneum is similar in all genera, though wider in the fossil, as in *Ochotona*. The bone tapers distally in *Palaeolagus*, whereas it is approximately cubical in the Recent forms. The distal facet is broad and low in *Lepus*, but high and relatively narrow in *Palaeolagus*. This indicates a less firm union of the metatarsals with the tarsals than in the living forms. The ventral side of the bone is also rather different. On the median surface, the cuboid of *Palaeolagus* is hollowed out in the same manner as is that of *Lepus*.

No specimens of the *navicular* have been seen in any of the available collections, nor have any been described in the literature, so far as I am aware.

The *ectocuneiform* is rather like that of the living genera except for the proportionate differences in size. Its distal end is shaped to fit the end of the third metatarsal of *Lepus*, being broad dorsally and pinched ventrally. In other respects, also, the bone is very like that of *Lepus*.

The *metatarsals* appear to be almost identical in shape with those of *Lepus*, differing chiefly in their smaller size. Part of this difference is due to the difference in size of the respective animals, but the metatarsals of *Palaeolagus* appear to have been proportionately much shorter than those of the living leporids, and slightly shorter than those of *Ochotona*. Metatarsal V is almost identical with that of *Lepus*. The long proximal process articulates in the same manner with the lateral margin of the cuboid. The facets for the distal end of the cuboid and for metatarsal IV are almost identical to those of *Lepus*. Very little of the shaft is preserved. As may be told from the facets on the adjoining bones, the proximal ends of metatarsals III and IV are also almost identical in pattern to those of *Lepus*. Nothing is known of the size and relationships of the first two metatarsals, but it is very probable that the hallux was nearly as much reduced in *Palaeolagus* as it is in living lagomorphs.

From what little is preserved of them, the phalanges do not appear to differ from those of the living forms except in their actually (and perhaps proportionately) smaller size.

In summary, the skeleton of *Palaeolagus* is certainly that of a leporid, differing from the skeletons of the Recent members of the family less than it does from that of the pika. In all the characters in which it differs from those of the modern leporids, the skeleton of *Palaeolagus* is more primitive and less adapted for the leaping habitus than are the skeletons of the later forms. Most of the points in which the *Palaeolagus* skeleton is more similar to that of *Ochotona* than to those of living leporids seem to be points in which both genera are relatively similar to the primitive lagomorphine stock. As to its habits, it is believed that *Palaeolagus* must have been rather like the pika, and to have progressed either by "a series of short, quick hops" (Camp and Borell, 1937, p. 315), as does the pika, or less probably, to have been a scampering form, such as is *Neotoma* today. It seems very probable that the limb muscles of *Palaeolagus* agreed with those of *Ochotona* in their tendency towards fleshy rather than tendinous insertions. The muscles were probably not as fully differentiated as are those of the modern leporids, again agreeing with *Ochotona*. These, of course, are merely primitive conditions, and definitely should not be taken as indicative of special affinities between *Palaeolagus* and the ochotonids. The muscles were probably pale, as are those of *Ochotona* and *Sylvilagus*, rather than dark red as in *Lepus*. This indicates that they give more rapid action but less speed and endurance in the first two genera (and presumably in *Palaeolagus*) than in *Lepus* (Camp and Borell, 1937, p. 317). The presence of the initial stages of the leporid specializations suggests that the fossil was able to hop in a similar manner, though the great relative weakness of the skeleton and particularly of the attachments for the muscles definitely indicates that *Palaeolagus* was not an animal which sought safety by sustained flight. The Great Plains in the Oligocene were not the open plains that they have since become, but supported a considerable growth of trees, and clumps of bushes were probably scattered rather generally over the countryside. *Palaeolagus* probably lived in these clumps of bushes, wandering out in search of food, but usually not going so far away that a few quick hops and two or three dodges would not return him to safety. "The muscles and bones of the hind limb in *Lepus* combine those principles that result in great speed and endurance, whereas these structures in *Ochotona* and *Sylvilagus* are adapted to produce quickness of motion but neither great leaping ability nor endurance" (Camp and Borell, 1937, p. 326). *Palaeolagus* very definitely belongs in the latter category. The marked limitations of the present range of *Ochotona*

indicate that it would not be able to survive in a plains facies, where rapid running would be necessary to reach a safe hiding place. It is unquestionable that the increasing aridity of the plains during the later Tertiary brought about a reduction in the number of places in which the rabbits could take refuge, and that as a result those individuals, races, species or genera that were the best adapted for sustained flight had an increased survival rate. There would therefore be a positive selection of those mutations that tended to increase the rapidity of the animal's running and its endurance. The proportionately smaller size of the orbit in the fossil than in the Recent forms definitely indicates that *Palaeolagus* was not especially adapted for nocturnal life.

"Many of the characters of *Palaeolagus* . . . are those to be expected in a primitive type of rabbit. Among simple characters exhibited by this fossil form may be mentioned small size, skull short in proportion to its length, skull relatively low and flat, plane of the occiput forming only a slight angle with the plane of the palate, supraorbital processes small and of a simple type; air passages small, palate long, enamel folding on the teeth simple, muscle attachments on the mandible and on the femur weakly developed. Notwithstanding its large number of simple characters *Palaeolagus* . . . is characteristically a leporid, with the characteristic rabbit type of skull and skeleton and with the usual rabbit type of teeth, though with . . . differences in enamel pattern" (Dice, 1933, p. 306).

**Palaeolagus haydeni** Leidy

*Palaeolagus haydeni* Leidy: Proc. Acad. Nat. Sci. Phila., Vol. VIII, 1856.

*Palaeolagus agapetillus* Cope, 1873*a* (*nec P. agapetillus* Cope of Matthew 1902 and Schlaikjer 1935).

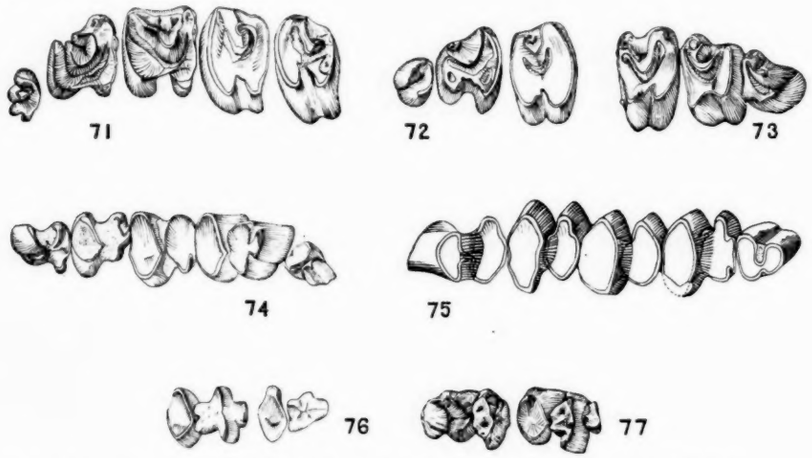



Fig. 71. *Palaeolagus haydeni*. Amer. Mus. Nat. Hist. No. 12,266. P$\underline{2}$–M$\underline{2}$ left.
Fig. 72. *P. haydeni*. Amer. Mus. Nat. Hist. No. 12,266. M$\underline{1}$–$\underline{3}$ right. Anterior end to the right.
Fig. 73. *P. haydeni*. Amer. Mus. Nat. Hist. No. 5684. dP$\underline{2}$–$\underline{4}$ right. Anterior end to the right.
Fig. 74. *P. haydeni*. Holotype of *P. agapetillus*, Amer. Mus. Nat. Hist. No. 5685. P3–M3 left.
Fig. 75. *P. haydeni*. Lectoholotype, Acad. Nat. Sci. Phila., No. 11,031. P3–M3 right.
Fig. 76. *P. haydeni*. Amer. Mus. Nat. Hist. No. 5681. M$\overline{1}$–2 left. M$\overline{1}$ erupted but unoccluded; M2 unerupted.
Fig. 77. *P. haydeni*. P. O. McGrew No. 101. dP3–$\overline{4}$ right.
All figures × 5.

*Tricium avunculus* Cope 1873*c*.
*Tricium leporinum* Cope 1873*c*.
*Tricium annae* Cope 1873*b*.
*Palaeolagus haydeni agapetillus* Cope, Troxell 1921.
*Protolagus affinus* Walker 1931*b*.
*Archaeolagus striatus* Walker 1931*b*.
*Palaeolagus hydeni* Leidy, Schlaikjer 1935.

Figs. 71–77; Cope, 1885, Pl. LXVI, Figs. 1–26; Troxell, 1921, Figs. 1–20; Dice, 1933, Figs. 10–12 and Pls. XXV–XXVI; and Dice and Dice, 1935, Figs. 7–26 and Pl. XCIII.

*Lectoholotype:* Since no type has ever been selected, I hereby choose Acad. Nat. Sci. Phila., No. 11,031, a lower jaw with $P\overline{3}$–$M\overline{3}$ left, as the lectoholotype. This appears to have been one of Leidy's original specimens, having been figured by him in 1869.

The teeth are high crowned and the enamel cap is so greatly reduced that it wears away with extreme rapidity, much faster than in *P. temnodon*. In the latter, $M\underline{1}$ is only slightly worn when $M\underline{3}$ is erupting, whereas, in the former, it is considerably worn, and $M\underline{2}$ is the one that is slightly worn. The crown is covered with a thick layer of cement,

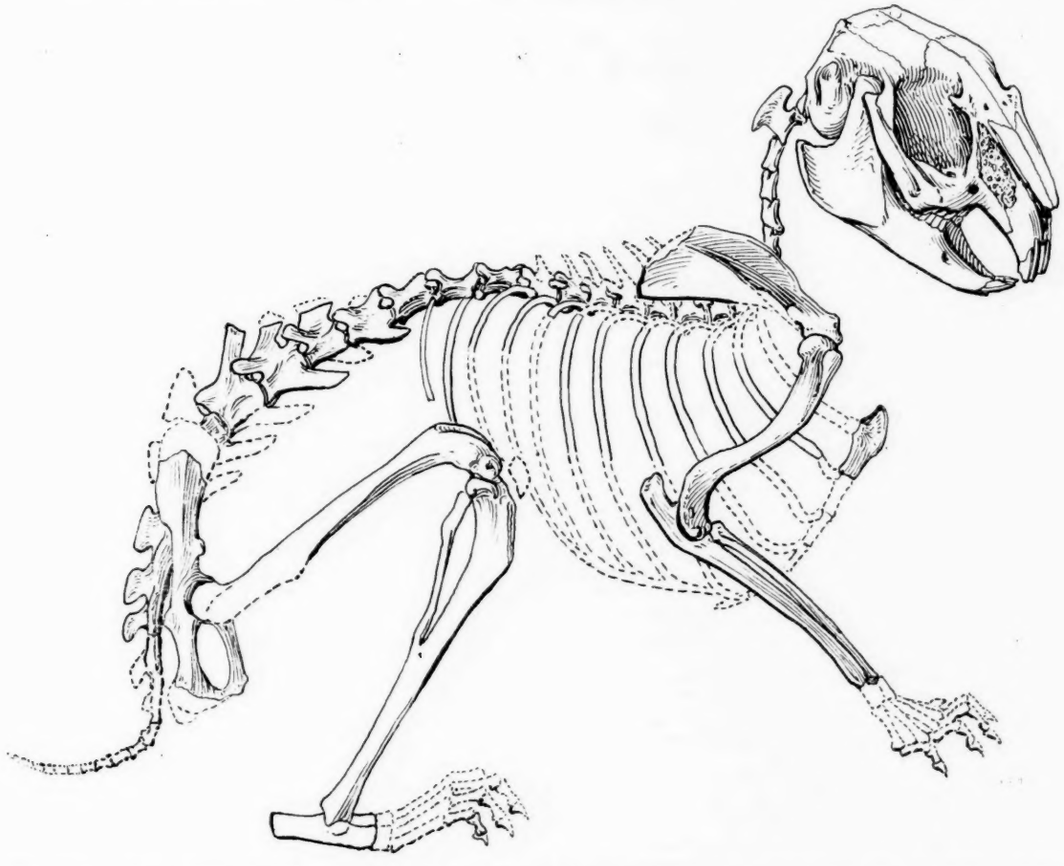


Fig. 78*a*. *Palaeolagus haydeni*. Skeleton from the right, based on Univ. Michigan No. 14,317. $\times \frac{2}{3}$.

which is deposited over the whole tooth, except for the tips of the cusps, beginning slightly before the time the tooth erupts from the alveolus. Crenulations are present in the hypostria for a short time. The buccal lobes of P$\underline{2}$ and dP$\underline{2}$ are reduced in size. The enamel seems to be incomplete on the crowns of some of the unerupted upper premolars, as in *Hypolagus*, a distinction from *P. temnodon*. The pit at the postero-external corner of the deciduous molars is clearly marked. The upper molars are beginning to show definite signs of transverse elongation. The hypostria lasts as a definite fold after the crescent has been worn away. The two lobes of M$\underline{3}$ are united before the tooth has erupted. The union of the talonid and trigonid in P$\bar{3}$ has migrated an appreciable distance toward the buccal margin of the tooth, whereas in *P. temnodon* it is almost exactly in the center of the tooth. The crown pattern of the talonid of the lower molars is even more aborted than in *P. temnodon*. Since practically all the known skeletal material of the genus belongs to this species, no distinctions are possible, based on that part of the animal.

The tooth measurements vary extremely with the age of the animal in all of the Oligocene lagomorphs. It is, in addition, impossible to pick a definite point from which to take all measurements, unless the place measured is the wear surface. The figures given below are based on the diameters of the worn surfaces. These, of course, are not

*Palaeolagus haydeni*

MEASUREMENTS OF CHEEK TEETH—UPPER TEETH

All measurements in millimeters

| | *Amer. Mus. Nat. Hist. No. 5684* | *Amer. Mus. Nat. Hist. No. 12,266a* | *Amer. Mus. Nat. Hist. No. 12,266b* |
|---|---|---|---|
| P$\underline{2}$ antero-posterior | 1.02d | | 0.91 |
| width | 1.37d | | 1.46 |
| P$\underline{3}$ antero-posterior | 1.52d | | 1.80 |
| width protoloph | 1.57d | | 1.38 |
| width metaloph | 2.06d | | 2.18 |
| P$\underline{4}$ antero-posterior | 1.68d | | 2.02 |
| width protoloph | 1.92d | | 1.80 |
| width metaloph | 1.95d | | 2.29 |
| M$\underline{1}$ antero-posterior | | 1.85 | 1.74 |
| width protoloph | | 2.34 | 2.46 |
| width metaloph | | 2.05 | 2.22 |
| M$\underline{2}$ antero-posterior | | 1.68 | 1.68 |
| width protoloph | | 1.98 | 2.05 |
| width metaloph | | 1.42 | 2.03 |
| M$\underline{3}$ antero-posterior | | 0.68 | |
| width | | 0.91 | |

d = deciduous tooth.

LOWER TEETH

| | *Lectoholotype, Acad. Nat. Sci. Phila. No. 11,031* | *Amer. Mus. Nat. Hist. No. 5685. Holotype, P. agapetillus* | *Amer. Mus. Nat. Hist. No. 5681* | *P. O. McGrew No. 102* | *P. O. McGrew No. 101* | *P. O. McGrew No. 103* | *P. O. McGrew No. 104* |
|---|---|---|---|---|---|---|---|
| $P\overline{3}$ antero-posterior | 2.00 | 1.43 | | 2.29d | 2.47d | 2.49d | 2.57d |
| width trigonid | 1.39 | 1.03 | | 1.41d | 1.42d | 1.46d | 1.54d |
| width talonid | 1.85 | 1.41 | | 1.79d | 1.66d | 1.72d | 1.98d |
| $P\overline{4}$ antero-posterior | 2.04 | 1.67 | | 2.48d | 2.34d | 2.50d | 2.44d |
| width trigonid | 2.21 | 1.27 | | 1.52d | 1.57d | 1.68d | 1.63d |
| width talonid | 1.82 | 1.21 | | 1.65d | 1.70d | 1.72d | 1.75d |
| $M\overline{1}$ antero-posterior | 2.21 | 1.82 | 2.25 | | | | |
| width trigonid | 2.09 | 1.86 | 1.40 | | | | |
| width talonid | 1.84 | 1.62 | 1.48 | | | | |
| $M\overline{2}$ antero-posterior | 2.04 | 1.82 | 1.96 | | | | |
| width trigonid | ca. 2.20 | 1.72 | 1.54 | | | | |
| width talonid | 1.85 | 1.42 | 1.12 | | | | |
| $M\overline{3}$ antero-posterior | 1.32 | 0.81 | | | | | |
| width trigonid | 1.32 | 0.94 | | | | | |
| width talonid | 0.89 | 0.62 | | | | | |

d = deciduous tooth.

homologous parts of the teeth when the individuals are of different ages. There is no standard diameter that can be measured in unworn teeth. The figures in the accompanying table merely show part of the range of variation with age, since no attempt has been made to include all stages of wear. Measurements of old individuals, especially, have not been included in the tables. It is believed, however, that the presentation of measurements will be of some benefit, even if only to show the variability of the teeth, and the danger of erecting species of lagomorphs on size alone. In the drawings, the crowns of the lower cheek teeth have all been rotated into the same plane, since otherwise it would be impossible to show the crown pattern of more than two teeth in the same figure.

*Horizon:* Middle and Upper Oligocene of the Great Plains. Cope (1884, p. 881) states that some of the John Day material appeared to him indistinguishable from *P. haydeni*, and rather different from *Archaeolagus ennisianus*. This material has not been studied in connection with this paper, but Matthew (1901, p. 376) states that all specimens from the John Day have the archaeolagine type of $P\overline{3}$, and apparently the material to which Cope referred merely represents a small variety of *Archaeolagus ennisianus*.

**Palaeolagus temnodon** Douglass

*Palaeolagus temnodon* Douglass, Trans. Amer. Philos. Soc., N.S., Vol. XX, 1901.

Figs. 78–91

*Lectoholotype:* Carnegie Museum No. 725a.

In the upper molars, the crescent is much less lasting than in *P. haydeni*, and a lake develops, representing the buccal part of the hypostria, lying between the crescent and the lingual margin of the tooth. The crowns are appreciably lower than in *P. haydeni*. The cement covering is not as heavy as in the latter form, and it is deposited slightly later. $P\underline{2}$ is, of course, composed of a trefoil. The buccal lobe is more lasting than in *P. haydeni*, remaining through a large part of the animal's life. In unworn specimens, $P\underline{3}$ is much less advanced even than in *Mytonolagus*. The anterior ridge extends across no more than half the tooth, and is quite sharply divergent from the posterior crest, instead of being nearly parallel to it as in *Mytonolagus* (Burke, 1934, Pl. L, Fig. 5). $P\underline{4}$ also seems less molariform than in *Mytonolagus*. In the latter, there is a marginal crest on the anterior, lingual and posterior sides, which is beginning to extend along the external side, and the central V is connected posteriorly with the external end of the posterior crest and anteriorly with the external end of the anterior one. Burke has mentioned (1934, p. 404) the weakness of the hypostria, but has not stressed its apparent secondary nature. From the appearance of the specimens, the hypostria seems to have been formed after the complete development of the protocone-hypocone crest along the lingual margin of the tooth. This may, of course, merely be an adaptation to a better ontogenetic development of the tooth. Crenulations have not been observed in the hypostria of any of the molars of this species. The upper molars are not developing in a transverse direction as are those of the later species. The tooth measurements are as variable as are those of *P. haydeni*.

$M\underline{3}$ is sometimes as much reduced as in *Desmatolagus*. Its pattern is very variable, which, together with its small size, strongly indicates degeneracy, and suggests that although in most respects *P. temnodon* is a good structural ancestor of *P. haydeni*, it may not be a direct genetic ancestor. There is a faint crest, running down the posterior side of the tooth. If the tooth is seen in exactly the right stage of wear, this appears as a posterior lobule, similar to that at the rear of slightly worn lower cheek teeth. This appears never to be present in *P. haydeni*.

Even in as primitive and low crowned a species as is this one, the bases of the cheek tooth prisms penetrate into the orbit to form a marked prominence.

Apparently the first stage in the deposition of cement in this species is the spreading of a thin film over the entire surface of the crown, except for the tips of the cusps. After this uniform film has been deposited, the deposition of cement is continued in the valleys, and the deposition continues until the valleys are filled.

There is considerable variation in the pattern of $P\overline{3}$ when unworn or in the early stages of wear. Some of these variants are shown in the figures (Figs. 86–91). Part of this is a wear feature, due to slightly different angles at which the teeth may be set in the jaw, so that different parts are worn to different amounts in the initial stages. It seems to me that a more important cause of the variability is the degeneracy and entire loss of function of the pattern-bearing portion of the crown. Of course, the degeneracy can have no effect

in causing the variation, but it would obviously permit natural selection to cease acting on variations in the details of the crown pattern, so that mutations modifying this uppermost portion of the tooth would be free to develop in any manner they desired. Since the pattern-bearing portions of the teeth no longer have any functional importance, no varia-

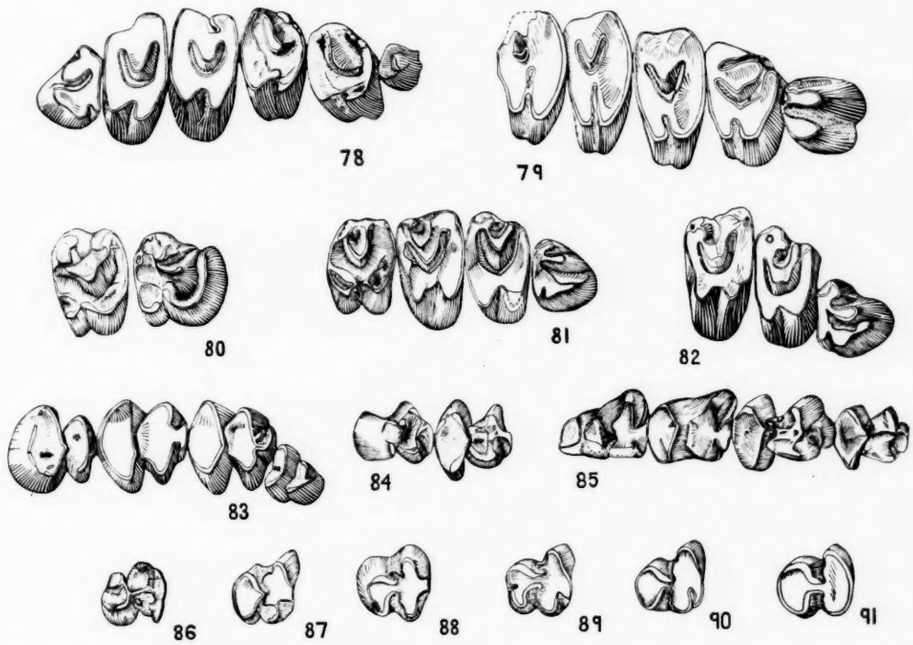



Fig. 78. *Palaeolagus temnodon.* Amer. Mus. Nat. Hist. No. 8051. dP$\underline{3}$–M$\underline{3}$ left.
Fig. 79. *P. temnodon.* Amer. Mus. Nat. Hist. No. 8053. P$\underline{2}$–M$\underline{2}$ right. Anterior end to the right.
Fig. 80. *P. temnodon.* A. E. W. No. 9094. P$\underline{3}$–$\underline{4}$ right. Anterior end to the right.
Fig. 81. *P. temnodon.* A. E. W. No. 9229. dP$\underline{2}$–M$\underline{1}$ right. Anterior end to the right.
Fig. 82. *P. temnodon.* A. E. W. No. 9182. dP$\underline{2}$–$\underline{4}$ right. Anterior end to the right.
Fig. 83. *P. temnodon.* A. E. W. No. 9185. P$\bar{4}$–M$\underline{3}$ left.
Fig. 84. *P. temnodon.* Amer. Mus. Nat. Hist. No. 8052. P$\bar{3}$–$\bar{4}$ right.
Fig. 85. *P. temnodon.* Princeton Univ. No. 14,240. dP$\bar{3}$–$\bar{4}$, M$\bar{1}$–$\bar{2}$ right.
Fig. 86. *P. temnodon.* Amer. Mus. Nat. Hist., ex Nos. 9655–9657. P$\bar{3}$ left.
Fig. 87. *P. temnodon.* Amer. Mus. Nat. Hist., ex Nos. 9655–9657. P$\bar{3}$ right.
Fig. 88. *P. temnodon.* Amer. Mus. Nat. Hist., ex Nos. 9655–9657. P$\bar{3}$ right.
Fig. 89. *P. temnodon.* Amer. Mus. Nat. Hist., ex Nos. 9655–9657. P$\bar{3}$ right.
Fig. 90. *P. temnodon.* Amer. Mus. Nat. Hist., ex Nos. 9655–9657. P$\bar{3}$ right.
Fig. 91. *P. temnodon.* Amer. Mus. Nat. Hist., ex Nos. 9655–9657. P$\bar{3}$ right.
All figures × 5.

tions in the pattern would be likely to have either a positive or a negative survival value. Variations of the sort here illustrated, therefore, are considered to have no taxonomic significance.

M$\bar{1}$ is like dP$\bar{4}$ of *P. haydeni*, with a basined trigonid, surrounded by crests, and a very cuspidate talonid, with a distinct third lobule, at an appreciably lower elevation. The talonid is not as uniformly lophate as in the milk tooth of *P. haydeni*, and the accessory cuspules are more irregularly scattered.

$M\bar{2}$ of one specimen of this species, Princeton Univ. No. 14,240, is quite unusual (Fig. 85). The trigonid is similar to that of $M\bar{1}$, although its anterior face is not as high as in that tooth. Most remarkable, however, is the fact that the talonid is higher than the trigonid. This may be an aberrant specimen, since no trace of this condition is visible in A.E.W. No. 9185, an animal of about the same age. The hypoconid and entoconid are larger and more distinct than in $M\bar{1}$, and there appear to be only two other main cuspules in the talonid basin, though there are some minor ones. The hypoconulid has cingular arms running toward the lingual side—one from its anterior margin and one from its posterior.

There is a more separate posterolophid in $dP\bar{3}$ than in the corresponding tooth of *P. haydeni*. This crest is united medially with the hypolophid, but is separate at both ends instead of merely at the lingual end as in *P. haydeni*. $DP\bar{4}$ is nearly alike in the two species.

Practically no cement is present any place on the lower teeth. On the uppers, it is much more restricted than in *P. haydeni*. It is usually limited, in all teeth, to a small amount in the valleys of both the permanent and the deciduous teeth.

*Palaeolagus temnodon*

MEASUREMENTS OF CHEEK TEETH—UPPER TEETH

(All measurements in millimeters. Figures are diameters of wear surfaces)

| | | *A.M.N.H. No. 9655–57* | *A.M.N.H. No. 8051* | *A.M.N.H. No. 9655–57* | *A.M.N.H. No. 9655–57* | *A.M.N.H. No. 9655–57* | *A.M.N.H. No. 9655–57* | *A.M.N.H. No. 9655–57* | *A.M.N.H. No. 9655–57* | *A.M.N.H. No. 9655–57* | *A.M.N.H. No. 8053* | *A.M.N.H. No. 9655–57* | *A.M.N.H. No. 9655–57* | *A.M.N.H. No. 9655–57* | *A.E.W. No. 9094* | *A.E.W. No. 9182* | *A.M.N.H. No. 9655–57* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| P2 | antero-posterior | | 1.23 | | | 1.10 | | | | 1.10 | 1.20 | 1.17 | 1.47 | | | 1.53d | 1.60d |
| | transverse..... | | 2.39 | | | 1.87 | | | | | 1.65 | 1.88 | 2.19 | | | 1.88d | 2.24d |
| P3 | antero-posterior | | 2.15 | 2.04 | 1.96 | 2.07 | 1.96 | 1.98 | | 2.12 | 2.05 | 1.94 | 2.21 | 2.08 | 2.08 | 1.65d | 1.80d |
| | width protoloph | | 2.58 | | 3.20 | 2.99 | 2.58 | 2.87 | | | 2.44 | 2.48 | 2.58 | 2.23 | 1.78 | 1.99d | 2.99d |
| | width metaloph | | 3.51 | | 3.82 | 3.08 | 3.37 | 3.52 | | 2.83 | 2.70 | 3.21 | 3.57 | 2.97 | 2.27 | 2.65d | 3.67d |
| P4 | antero-posterior | 2.04 | 2.08 | 1.99 | 2.16 | 2.28 | 2.12 | 1.92 | 2.10 | 2.15 | 2.09 | 2.18 | 2.24 | 2.08 | 2.14 | 1.95d | 1.96d |
| | width protoloph | 4.11 | 3.62 | 3.45 | 4.54 | 3.76 | 3.26 | 3.47 | 3.61 | 2.81 | 3.13 | 3.30 | 3.53 | 3.23 | 2.37 | 2.55d | 3.57d |
| | width metaloph | 3.81 | 3.64 | 3.43 | 4.06 | 3.64 | 2.82 | 4.26 | 3.59 | 3.02 | 3.07 | 3.39 | 3.42 | 3.25 | 2.47 | 2.32d | 3.60d |
| M1 | antero-posterior | 1.75 | 1.94 | 1.82 | 1.91 | 1.91 | 2.05 | 1.66 | 1.94 | | 1.82 | 2.01 | 1.88 | 2.05 | 1.96 | | 1.89 |
| | width protoloph | 4.25 | 3.56 | 3.34 | 3.57 | 3.65 | 3.14 | 3.55 | 3.57 | | 3.24 | 3.25 | 3.45 | 3.21 | 2.62 | | 2.38 |
| | width metaloph | 3.16 | 3.35 | 3.19 | 3.69 | 3.31 | 2.89 | 3.73 | 3.19 | | 3.04 | 3.17 | 3.34 | 3.12 | 2.31 | | 2.28 |
| M2 | antero-posterior | 1.66 | 1.81 | 1.77 | 1.73 | 1.86 | | 1.62 | 1.72 | | 1.97 | 1.92 | 1.87 | 1.90 | 1.88 | | 1.84 |
| | width protoloph | 3.60 | 3.10 | 3.08 | 3.49 | 3.17 | | 3.40 | 3.03 | | 3.04 | | 3.32 | 3.13 | 2.44 | | 2.18 |
| | width metaloph | 2.83 | 2.67 | 2.84 | 2.92 | 2.46 | | 2.68 | 2.60 | | | 2.62 | 2.58 | 2.64 | 1.98 | | 1.95 |
| M3 | antero-posterior | | 0.97 | | | | | 0.89 | 0.90 | | | | | 0.81 | 0.98 | | 0.95 |
| | transverse..... | | 1.54 | | | | | 1.65 | | | | | | 1.40 | 1.63 | | |

d = deciduous tooth.

MEASUREMENTS OF CHEEK TEETH—LOWER TEETH

(in millimeters)

| | *A.E.W. No. 9185* | *Princeton Univ. No. 14,240* | *Amer. Mus. Nat. Hist. No. 8052* | *Amer. Mus. Nat. Hist. No. 9655–57* | *Amer. Mus. Nat. Hist. No. 9655–57* | *Amer. Mus. Nat. Hist. No. 9655–57* | *Amer. Mus. Nat. Hist. No. 9655–57* | *Amer. Mus. Nat. Hist. No. 9655–57* |
|---|---|---|---|---|---|---|---|---|
| P$\overline{3}$ antero-posterior | | 2.51d | 1.48 | 1.82 | 2.15 | 1.75 | 1.93 | 1.76 |
| width trigonid | | 1.40d | 1.01 | 1.23 | 1.44 | 1.12 | 1.21 | 1.30 |
| width talonid | | 1.70d | 1.53 | 1.80 | 1.89 | 1.70 | 1.81 | 1.68 |
| P$\overline{4}$ antero-posterior | 2.07 | 2.33d | 2.20 | 2.48 | 2.32 | 2.26 | 2.32 | 2.24 |
| width trigonid | 1.95 | 1.58d | 1.68 | 2.14 | 2.35 | 2.00 | 2.15 | |
| width talonid | 1.54 | 1.65d | 1.45 | 1.88 | 1.97 | 1.83 | 1.91 | 1.72 |
| M$\overline{1}$ antero-posterior | 2.62 | 2.53 | | 2.66 | 2.53 | 2.44 | 2.37 | 2.56 |
| width trigonid | 2.17 | 1.77 | | 2.27 | 2.38 | 2.18 | 2.13 | |
| width talonid | 2.07 | 1.92 | | 2.08 | 2.07 | 2.04 | 1.94 | 2.00 |
| M$\overline{2}$ antero-posterior | 2.57 | 2.07 | | | 2.32 | 2.33 | 2.43 | 2.49 |
| width trigonid | 2.04 | 1.70 | | | 2.31 | 1.98 | 2.14 | 2.37 |
| width talonid | 1.79 | 1.52 | | | 2.06 | 1.85 | 1.95 | 1.87 |
| M$\overline{3}$ antero-posterior | 1.22 | | | | 1.36 | 1.10 | | |
| width trigonid | 1.26 | | | | 1.44 | 1.07 | | |
| width talonid | 0.96 | | | | 1.04 | 0.77 | | |

d = deciduous tooth.

The cranial border of the scapula curves forward much more markedly than in *P. haydeni*. The neck is the same width in both species, but the bone is much shorter and broader in *P. temnodon*. The spine extends to the neck and misses the glenoid by less than one centimeter. The glenoid is flatter than in *P. haydeni*, and very much flatter than in *Lepus*.

The only other skeletal remains that are certainly referable to this species are ends of some of the limb bones and a number of calcanea and astragali. These show no appreciable difference from those of *P. haydeni.*

*Horizon and Localities:* Lowest Oligocene of Pipestone Springs and Three Forks, Montana. The Three Forks material in the collection of Mr. C. A. Kinsey is absolutely indistinguishable from the material from Pipestone. The Cypress Hills material probably belongs to this species, but is discussed in more detail below.

### **Palaeolagus** cf. **temnodon**

The material from the Cypress Hills is unfortunately so extremely fragmentary, and the teeth are in such advanced stages of wear, that it is almost impossible to make any certain determinations as to its specific identity. As far as can be told from the available material, it seems to belong either to *P. temnodon* or to a species which is indistinguishable from it on the basis of the known material, though there appears to be some variation in size which might indicate the presence of two species. This material consists of four specimens of isolated cheek teeth in the collections of the Canadian National Museum, and two in my private collection, collected by Drs. F. D. and H. E. Wood and Miss Rolena Dowden in 1934, and presented to me by them.

Cope (1885) originally described the Cypress Hills material and referred it to *Palaeolagus turgidus.* His later remarks (1889 and 1891) suggest that there was originally some material of that species present, though it must subsequently have been lost. I have seen no material remotely suggesting *Megalagus* from the Cypress Hills. Lambe (1908, p. 58)

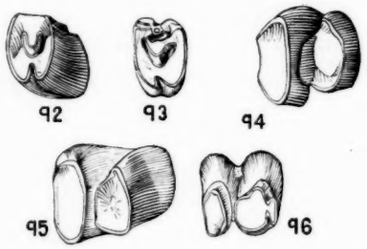



Fig. 92. *Palaeolagus* cf. *temnodon.* Can. Nat. Mus. No. 6484, right upper molar.
Fig. 93. *P.* cf. *temnodon.* Can. Nat. Mus. No. 6486. P4 or M1 right.
Fig. 94. *P.* cf. *temnodon.* Can. Nat. Mus. No. 6485. P4, M1 or M2 right.
Fig. 95. *P.* cf. *temnodon.* A. E. W. No. 9058*b.* P4, M1 or M2 right.
Fig. 96. *P.* cf. *temnodon.* A. E. W. No. 9058*a.* P4, M1 or M2 right.
All figures × 5.

referred the material to *P. haydeni.* Russell (1934, p. 57) referred it to *P. temnodon,* to which species the material probably belongs. (See Figs. 92–96.) The teeth agree with those of *P. temnodon* in being very much shorter crowned than are those of *P. haydeni,* one specimen (A.E.W. No. 9058*a*) showing the hypoconulid lobe and the roots at the opposite ends of the same tooth, a situation which never occurs in *P. haydeni* or any of the later species of the genus. The incisors associated with Can. Nat. Mus. No. 6484 are not those of *Palaeolagus,* but are referable to some rodents. The same is true of the incisor with Can. Nat. Mus. No. 6486, which is that of a cylindrodont. The incisor with Can. Nat.

Mus. No. 6485 is that of a lagomorph, and is undoubtedly conspecific with the cheek teeth. Can. Nat. Mus. No. 6491 is an incisor, labelled as *Palaeolagus*, which appears to be referable to *Titanotheriomys*.

Although this material is so fragmentary, there is but little question about its reference to *P. temnodon*. It will, of course, require more complete material definitely to establish that it belongs to that species, but it can certainly be stated that the Cypress Hills material does not belong to any other known species of the genus. The known Cypress Hills material is definitely not referable to *Megalagus*.

*Palaeolagus cf. temnodon*

MEASUREMENTS IN MILLIMETERS

| | *Can. Nat. Mus. No. 6484* | *Can. Nat. Mus. No. 6485* | *Can. Nat. Mus. No. 6486* | *A.E.W. No. 9058A* | *A.E.W. No. 9058B* |
|---|---|---|---|---|---|
| $M\underline{1}$? antero-posterior | 2.01 | | 2.20 | | |
| width protoloph | 2.88 | | 3.20 | | |
| width metaloph | 2.65 | | 3.26 | | |
| $M\bar{1}$? antero-posterior | | 2.47 | | 2.14 | 2.14 |
| width trigonid | | 2.48 | | 1.58 | 2.32 |
| width talonid | | 2.04 | | 1.57 | 1.90 |

*Horizon and Locality:* Lower Oligocene of the Cypress Hills, Saskatchewan.

**Palaeolagus burkei** n. sp.

*Palaeolagus* ? *agapetillus* Cope of Matthew 1902.
*Palaeolagus agapetillus* Cope, Schläikjer 1935.

Fig. 97

*Holotype:* Amer. Mus. Nat. Hist. No. 8704.

There is a group of specimens of *Palaeolagus* which seem to represent a valid and as yet undescribed species. Nothing could be more appropriate than to name it for Mr. J. J. Burke, to whose works I am indebted for much of my information about the evolution of the early lagomorphs.

In this species, the skull is flat; the braincase is not inflated by the swelling of the brain; the basifacial axis is not bent on the basicranial axis; the snout is very slender; and the cheek teeth are very small, with a thin coating of enamel. This species is represented by A.M.N.H. No. 8704, a rather good skull, and A.M.N.H. No. 8714, a maxilla, both from northeast Colorado, as well as other specimens from South Dakota and Wyoming. Matthew (1902, pp. 307–308) hesitantly referred these specimens to Cope's species *P. agapetillus*. Since these specimens both have worn upper cheek teeth, whereas the holotype of *P. agapetillus* is a mandible with partly erupted permanent premolars and slightly worn molars, it is difficult to make direct comparisons. The holotype of *P. agapetillus* appears, however, to be absolutely identical with specimens of *P. haydeni* in the same stage of wear.

The teeth of Cope's specimen, moreover, are distinctly too large to occlude with those of the holotype of *P. burkei*.

In his later works, Cope reached the conclusion that *P. agapetillus*, like the species he referred to *Tricium*, was merely one stage of wear of *P. haydeni*, stating: "The last stage prior to maturity sees the first milk-molar shed, and the younger portion of the first permanent molar protruded. A specimen of this age furnished the basis of *Palaeolagus agapetillus*" (1884, pp. 877–878). It seems almost certain that he was correct in this allocation. Furthermore, even if *P. agapetillus* should turn out to be a valid species, I do not believe that the material now described as *P. burkei* could be referable to it. Matthew (1902, pp. 307–308) hesitantly referred these specimens to *P. agapetillus*. He states that "The species appears to be good, on the evidence of some half-dozen specimens referred to it and compared with the very numerous *P. haydeni* specimens in our collections. Whether the type of *P. agapetillus* is properly referable to it, I am unable to decide; but leave it provisionally" (op. cit., p. 308).

The skull is very flat, there being an angle of only seven degrees between the basicranial and the prolongation of the basifacial axes. In *P. intermedius*, this angle is twenty degrees; in *P. haydeni*, twenty-two degrees; in *Archaeolagus ennisianus*, thirty-three degrees, and in *Lepus campestris*, forty-seven degrees (Matthew, 1902, p. 307). The orbit is small and high on the face. The snout is short and slender. The bones of the snout are more fenestrate than in *P. haydeni*. The brain is entirely unexpanded. The posterior nares are very narrow, the palatines extending across most of the usual opening. This animal must have had slight endurance, and therefore have been a very weak runner.

The hypostria is rather deep, and persists long after all trace of the buccal parts of the pattern has been lost. The enamel is thin, with practically no differentiation in thickness

Fig. 97. *Palaeolagus burkei* n. sp. Holotype. Amer. Mus. Nat. Hist. No. 8704. P$\underline{2}$–M$\underline{3}$ left. × 5.

between the different parts of the tooth. This is a primitive character, and sets this species apart from most of the other leporids. There are no crenulations in the hypostria. P$\underline{2}$ and M$\underline{3}$ are very small, and the buccal lobe of the former is extremely evanescent. The teeth are all very small, though quite high crowned.

This species appears in most respects to be either a persistently primitive form, or a pseudo-primitive one. In the reduction of P$\underline{2}$ and M$\underline{3}$, it appears to be definitely specialized. On the other hand, the fact that the basifacial axis has not been bent on the basicranial one, the small size of the brain, the shortness of the snout, the narrowness of the posterior nares, and the flatness of the skull, appear to be primitive lagomorph characters.

Schlaikjer refers a left maxillary with P$\underline{2}$–M$\underline{2}$, Mus. Comp. Zool. No. 2890, to *Palaeolagus agapetillus* Cope, as interpreted by Matthew. This specimen comes from the Upper Oligocene of southeastern Wyoming. Schlaikjer states that it "compares very closely with the neotype [sic] skull of this species described by Dr. Matthew . . . from the

*Leptauchenia* Beds of Logan County, Colorado, except that P4 is of slightly greater antero-posterior dimension. P2 and M3 are greatly reduced. . . ." (Schlaikjer, 1935, p. 127). This material seems from Schlaikjer's description to be definitely referable to *P. burkei* as here defined.

Although Schlaikjer (op. cit., p. 127) considered that this was the most specialized member of the genus *Palaeolagus sensu stricto*, I find myself unable to agree with him, for the reasons cited above. I believe that *P. burkei* is definitely not on the line leading to *Archaeolagus* or to any of the later leporids, and that it cannot be descended from any known Middle Oligocene species of the genus.

*Palaeolagus burkei*

MEASUREMENT OF UPPER CHEEK TEETH IN MILLIMETERS

| | | *Holotype, Amer. Mus. Nat. Hist. No. 8704* |
|---|---|---|
| P2 | antero-posterior | 0.97 |
| | width | 1.39 |
| P3 | antero-posterior | 1.55 |
| | width protoloph | 1.95 |
| | width metaloph | 2.96 |
| P4 | antero-posterior | 1.42 |
| | width protoloph | 2.87 |
| | width metaloph | 2.83 |
| M1 | antero-posterior | 1.38 |
| | width protoloph | 2.72 |
| | width metaloph | 2.70 |
| M2 | antero-posterior | 1.25 |
| | width protoloph | 2.47 |
| | width metaloph | 2.12 |
| M3 | antero-posterior | 0.63 |
| | width | 1.23 |

*Horizon and Range:* Leptauchenia Beds of northeast Colorado and eastern Wyoming and possibly Oreodon beds of South Dakota.

### **Palaeolagus intermedius** Matthew

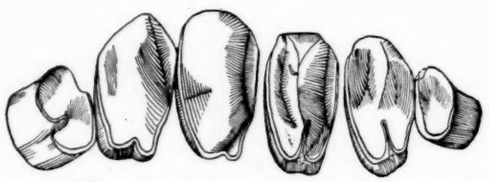
*Palaeolagus intermedius* Matthew, Bull. Amer. Mus. Nat. Hist., Vol. XII, 1899.
*Palaeolagus haydeni intermedius* Matthew, Troxell 1921.

Figs. 98–99

*Holotype:* Amer. Mus. Nat. Hist. No. 8722.

In his first real description of this form, Matthew describes it as follows: "*P. intermedius* Matthew, of intermediate size, with skull considerably shorter than in *P. haydeni*,

cranium rounder. Considerably smaller than *P. turgidus*, with more slender jaws and larger diastema. Fragments of limb bones indicate a skeleton of the size and proportions of *P. turgidus*, of which species it may prove to be a variety. Six specimens are referred here, No. 8722, a skull, being the type" (1901, p. 377). Later, he added to the above description the following: "Type, a nearly complete skull from the upper levels of the White River, at Castle Rock, Cedar Creek, Col. Associated type, upper and lower jaws and fragments of skeleton from same level and region. This skull is much more depressed on the basicranial axis than *P. agapetillus;* it has a long and heavy muzzle, unlike the slender, sharp muzzles of the two preceding species [*P. haydeni* and *P. agapetillus* = *P. burkei*]; the teeth are larger than those of *P. haydeni*, but resemble them in pattern; the length of the diastema is equal to that in *P. turgidus* but the teeth are much smaller, and of more *Lepus*-like pattern; the skeleton appears to be as large as that of *P. turgidus*, and of similar proportions. The postfrontal process is nearly as large as in *Lepus ennisianus;* the muzzle is of the same length as in that species, but heavier; the basifacial axis is somewhat less depressed, and the brain-case is distinctly smaller." (Matthew, 1902, pp. 308–309.) Troxell was apparently in doubt concerning the validity of this species, and finally made it a subspecies of *P. haydeni*, stating that "*P. agapetillus* and *P. intermedius* are apparently distinguishable from *P. haydeni* on the basis of size alone, and are here considered as subspecies" (Troxell, 1921, p. 348). The only other author who has made more than casual references to this species is Burke, who included this form as a valid species in the *Mytonolagus, brachyodon, turgidus* group (Burke, 1934, p. 405).



98

99

Fig. 98. *Palaeolagus intermedius.* Holotype. Amer. Mus. Nat. Hist. No. 8722. P2–M3 left.
Fig. 99. *P. intermedius.* Amer. Mus. Nat. Hist. No. 8572. P3–M3 left.
Both figures × 5.

The taxonomic position of this group of specimens has caused me considerable difficulty. There are undoubtedly some differences in the skull between the holotype and the typical *P. haydeni*. The face is more bent on the basicranial axis, and the brain case is more swollen, indicating an enlarging brain. The nasals do not extend beyond the incisors as do those of *P. haydeni*, and their posterior ends are slightly wider than in that form. The process of the premaxilla notching the maxillary just below the reticulate area is smaller than in the genotype. The interparietal is smaller than in *P. haydeni*, and the supraoccipital does not show in the dorsal view of the skull. The external auditory meatus

is directed more posterad than in the latter form. The teeth of the holotype and referred specimens are badly worn, but they all show a hypostria preserved after the entire loss of the crescentic lake. There is no trace of the lake isolated from the buccal end of the hypostria, which is so characteristic of *P. haydeni*. In this connection, Burke states that "the internal notch of the premolars . . . does not yet appear on any of the premolars to be of the type seen in . . . *Palaeolagus haydeni* Leidy, where, in addition to the internal groove, an external portion of the fold cuts downward into the crown and shows in an isolated enamel island on the worn premolars, as it does in the molars. The prevalence of the shallow internal fold in the premolars of the species which compose . . . the '*turgidus* group' . . . including . . . *brachyodon* . . ., *turgidus* . . . and *intermedius* . . ., contrasts strongly with the more transverse fold seen in the '*haydeni* group' " (Burke, 1934, p. 405). The specimens that I have seen, however, which Matthew referred to this species, seem to have a hypostria more like that of *Palaeolagus* than like that of *Megalagus* (see Fig. 98).

The characteristics of this form are such as thoroughly to justify the specific name that Matthew gave it. The skull agrees in most respects with that of *P. haydeni*. The teeth likewise appear to me to have more in common with that form than with *Megalagus*, in view of their prismatic, rootless nature, and the persistence of the hypostria. None of the material in the American Museum or elsewhere that I have seen seems to justify placing this species in *Megalagus*, although there are distinct suggestions in some of the material of a *Megalagus*-like $P\overline{3}$, which may, however, merely be due to the stage of wear which the tooth has attained in the available material. It is possible that this is a species of *Palaeolagus* which is tending toward *Archaeolagus*, and which has therefore paralleled *Megalagus* in the pattern of this tooth. This species, if it should eventually prove to be referable to *Megalagus*, would seem to be very much more specialized than any of the other members of the genus. Nevertheless, I have sufficient respect for Burke's opinions and the care with which he weighs his statements so that I would include this species in *Megalagus* on his authority alone, if he had specifically placed it there. However, although he has distinctly implied that this species belongs in *Megalagus* (since his use of the expression "*turgidus* group" in 1934 appears to be identical to his use of "*Megalagus*" in 1936), I consider it advisable for me to follow a conservative course, and leave this species in *Palaeolagus*. Its transfer to the other genus, if warranted, should be made by someone who has more first hand knowledge than do I of the details of lagomorph evolution.

Matthew's statements about the skeleton of this form do not carry great weight with me, since the skeleton is represented (at present, at least) merely by a few scraps. They appear to be slightly larger than most of the skeletal fragments of *P. haydeni*. Considering how little is known of the range of variation of the skeleton even of the latter type, they do not necessarily seem to be beyond the limits of variation of the genotype. It is almost useless to try to compare them with skeletal remains of *Megalagus*, since that genus is likewise represented only by fragments.

*Horizon and Locality:* Oreodon Beds, Castle Rock, Colorado. Specimens have been referred to this species from Nebraska and elsewhere.

*Palaeolagus intermedius*

MEASUREMENTS OF CHEEK TEETH IN MILLIMETERS

| | *Holotype, Amer. Mus. Nat. Hist. No. 8722* | | *Amer. Mus. Nat. Hist. No. 8752* |
|---|---|---|---|
| | *Left* | *Right* | |
| P$\underline{2}$ antero-posterior | 1.58 | 1.56 | |
| width | 2.48 | 2.32 | |
| P$\underline{3}$ antero-posterior | 2.22 | 2.13 | 2.18 |
| width protoloph | 3.36 | 3.32 | 2.93 |
| width metaloph | 4.01 | 3.80 | 3.43 |
| P$\underline{4}$ antero-posterior | 2.25 | 2.30 | 2.30 |
| width protoloph | 4.18 | 3.93 | 3.68 |
| width metaloph | 4.02 | 4.10 | 3.82 |
| M$\underline{1}$ antero-posterior | 2.05 | 2.08 | 2.20 |
| width protoloph | 3.61 | 3.78 | 3.78 |
| width metaloph | 3.61 | 3.70 | 3.67 |
| M$\underline{2}$ antero-posterior | 1.93 | 1.85 | 2.08 |
| width protoloph | 3.58 | 3.51 | 3.28 |
| width metaloph | 2.86 | 3.33 | 3.08 |
| M$\underline{3}$ antero-posterior | 1.10 | 1.12 | 0.69 |
| width | 2.07 | 2.04 | 1.36 |

| | *Amer. Mus. Nat. Hist. No. 8572* | | *Amer. Mus. Nat. Hist. No. 8572* |
|---|---|---|---|
| P$\bar{3}$ antero-posterior | 2.81 | M$\bar{2}$ antero-posterior | 2.99 |
| width trigonid | 2.12 | width trigonid | 2.92 |
| width talonid | 2.40 | width talonid | 2.50 |
| P$\bar{4}$ antero-posterior | 2.83 | M$\bar{3}$ antero-posterior | 1.66 |
| width trigonid | 2.68 | width trigonid | 1.55 |
| width talonid | 2.35 | width talonid | 1.38 |
| M$\bar{1}$ antero-posterior | 2.89 | | |
| width trigonid | 2.75 | | |
| width talonid | 2.48 | | |

**Palaeolagus hypsodus** Schlaikjer

*Palaeolagus hypsodus* Schlaikjer, Bull. Mus. Comp. Zool., Vol. LXXVI, 1935.

Although this species comes from the Lower Miocene, it is included here to complete the discussion of all forms that have been referred to *Palaeolagus*. Schlaikjer (1935, p. 126) gives the following specific characters. "About the size of *P. agapetillus* Teeth very hypsodont. P$\underline{3}$ almost quadrate in cross-section. P$\underline{4}$–M$\underline{2}$ oval in outline. Reentrant angles more compressed and proportionately more extensive than in the other species. Teeth almost entirely covered with cement." The quadrate P$\underline{3}$, with the deep

hypostria, seems more characteristic of *Archaeolagus* than of *Palaeolagus*. The same is true of the narrow, deep hypostria of the other teeth. The fact that the teeth are almost entirely covered with cement would tend to associate this form with *Archaeolagus*. If the teeth are more hypsodont than is normal in *P. haydeni*, it would also tend to associate this form with *Archaeolagus*. Although I have not had the opportunity to study the specimen, the specific diagnosis and Schlaikjer's figure (op. cit., Fig. 4) are so definitely in accord that there seems but little doubt that this form is referable to *Archaeolagus*. Since no other Lower Miocene *Archaeolagus* has been described from the Great Plains, there is little doubt that this species is valid, although no attempt has been made at the present time to determine its exact relationships, that being outside the scope of this work. Schlaikjer's tooth measurements indicate an animal about the same size as, or slightly smaller than, *P. haydeni*.

**" Palaeolagus " primitivus** (Schlaikjer)

*Hypolagus primitivus* Schlaikjer, Bull. Mus. Comp. Zool., Vol. LXXVI, 1935.
*Palaeolagus primitivus* (Schlaikjer), Wood 1937*a*.

This form, likewise from the Lower Miocene, is also discussed merely for completeness' sake. The holotype and only known specimen is unfortunately a very old animal. It is a large form, as large as *Megalagus*. The development of slight crenulations is similar to what takes place in some specimens of *Palaeolagus* or in *Archaeolagus*. The presence of buccal roots and the entire absence of cement (Schlaikjer, 1935, p. 128) indicates that this form cannot belong in either of these genera, and suggests that it is referable either to *Megalagus* or to a genus close to that form. The disappearance of the hypostria as a fold and the retention of its buccal end as a lake is characteristic of *Megalagus*, and is extremely different from any stages in the development of the pattern of *Palaeolagus*, *Archaeolagus* or *Hypolagus*. Without a more careful investigation of the question than is practicable at present, nothing certain can be stated of the generic allocation of this species. It seems certain that this animal does not belong in *Hypolagus*, as pointed out elsewhere (Wood, 1937*a*, pp. 39–40). It likewise does not belong in *Palaeolagus* as at present defined, its allocation to that genus in the previous paper being due to uncertainty at that time as to the validity of *Megalagus*. As at present visualized, Schlaikjer's species may belong in a new genus, in *Megalagus* or in *Desmatolagus*, but it is uncertain which. Since its reference to any one of these genera at the present time would be pure guesswork, it is considered best not to remove this species from *Palaeolagus* for the time being, in order not to complicate the nomenclature any more than is necessary, even though it is fully recognized that the present reference is incorrect.

**Leporid** gen. et sp. indet.

*Palaeolagus* ? sp., Wood and Wood, 1937.

This indeterminate material was referred to *Palaeolagus* because it was more like *P. haydeni* than like *Archaeolagus ennisianus*. In view of its apparent Lower Miocene age, it probably belongs to a Gulf Coast species of the latter genus.

**Megalagus** Walker

*Megalagus*, Walker: The Aerend, Vol. 2, No. 4, 1931.
*Genotype: Palaeolagus turgidus* Cope 1873c.

This genus is persistently low crowned, at least for a leporid. Buccal roots are always present on the upper molariform teeth. The hypostria is not as persistent as in *Palaeolagus*, wear destroying its lingual portion, except for a faint groove, and transforming its buccal end into a lake. The buccal end of the hypostria tends to lie in the posterior half of the tooth. The buccal lobe of $P\underline{2}$ is minute or absent. $P\underline{3}$ is not as molariform as in *Palaeolagus*. The valley between the buccal and central lobes is deep and persistent in $P\underline{4}$–$M\underline{2}$. The crescentic valley between the central and lingual lobes tends to open at the buccal side of the tooth for a long period of the animal's life, as in *Desmatolagus*. $P\overline{3}$ has a very shallow lingual fold, which disappears early in life, resulting in the pattern which Dice (1929) used to characterize the Archaeolaginae. This genus is very much larger than is *Palaeolagus*.

*Range:* Oligocene and possibly Lower Miocene of the Great Plains.

The *skull* of this genus is known only from fragments of the maxillary and palatine attached to series of upper cheek teeth. The palatine-maxillary suture is a rounded curve, apparently without the sharp anterior prolongation of the palatine seen in *Palaeolagus*. The anterior end of the palatine extends as far forward as the middle of $P\underline{4}$. The posterior palatine foramen lies directly across this suture. None of the available material shows the position of the posterior end of the incisive foramina, so that they must have ended anterad of $P\underline{3}$. The posterior nares extend forward to the middle of $M\underline{1}$. They were rather narrow. The palate was thus somewhat shorter than in *Palaeolagus*, the shortening having taken place at the expense of the palatine. This, of course, is a progressive character. The zygoma arises by the anterior end of $P\underline{4}$ in *M. brachyodon*, and by the middle of $P\underline{3}$ in *M. turgidus*. The deep pit on the anterior side of the zygoma, which characterizes *Palaeolagus*, is present in *M. turgidus* but not in *M. brachyodon*. The masseteric fossae appear somewhat more advanced than in *Palaeolagus*, which may merely be because of the larger size of *Megalagus*. The rest of the skull is unknown.

In spite of the fact that Walker recognized that *Palaeolagus turgidus* was quite distinct from *Palaeolagus haydeni*, his reasons for creating a new genus were not sufficient to convince most workers of the justice of his action. Most of the characters that he used are dependent entirely on the age of the animal, occurring in both *Palaeolagus* and *Megalagus*, though at different stages. There are, however, sufficient differences between the species referred to this genus and *P. haydeni* to warrant their generic separation, and Walker's name, of course, is valid. There is absolutely no justification for the erection of a subfamily for this genus at the present time.

The differences between the pattern of $P\overline{3}$ of this genus and of *Palaeolagus*, and the corresponding differences in the patterns of the upper teeth, do not indicate a fundamental difference in pattern between the two genera, but merely a diverse direction of development. With regard to $P\overline{3}$, *Megalagus* is merely more progressive than is *Palaeolagus*, the internal reentrant being limited to the uppermost portion of the crown, so that wear soon eliminates it. Enough is known of lagomorph evolution to indicate that the Middle Oligocene *Megalagus turgidus* and *Palaeolagus haydeni* could not have had a common

ancestor later than the Uinta, and that it was probably even earlier, since the Uinta *Mytonolagus* appears to belong to the *Megalagus* line, and probably was at least specifically separable from the Upper Eocene ancestors of *Palaeolagus*. There has never been any question of confounding the individual species of *Megalagus* with those of *Palaeolagus* nor has there been any trouble in allocating individuals to one genus or the other, except for the few specimens discussed under *Palaeolagus intermedius*. *Megalagus* (or the "*turgidus* group," which means the same thing) has, however, been made to include a number of specimens of a rather distinct type, which have only recently been shown by Burke to belong to the Mongolian genus *Desmatolagus*. As will be shown below, these forms are quite distinct from *Megalagus*, the tooth pattern being quite characteristic.

"The mandible is more robust than in *P. haydeni*, but has much the same form. The anterior mental foramen is behind the middle of the diastema, on its superior aspect, and the posterior is below the second molar [= $P\overline{4}$], *below* the middle of the ramus. The dental foramen is *above* the middle line of the ramus; the last-named two foramina having relations the reverse of that seen in *P. haydeni*" (Cope, 1884, p. 883). No specimens have been seen in which the angle and the ascending ramus are preserved. The masseteric fossa appears to have the same limits and to be of the same size as in *Palaeolagus*. The ventral border of the hinder third of the mandible appears to curve ventrad, as in the modernized leporids and in contrast with *Palaeolagus*. There are a large number of nutritive foramina on the lingual side of the mandible, concentrated over the knob marking the base of the incisor. Cope used these foramina as one of the main diagnostic features of *P. turgidus*, stating that there is a porous enlargement of the inner surface of the ramus just behind the symphysis (Cope, 1873*c*). There is no trace of fenestration on the lateral face of the mandible. As in *Palaeolagus*, there are two mental foramina, one beneath the posterior part of $P\overline{4}$ and the other in the diastema, almost on the top of the bone. The sharp ridge along the top of the diastema, which is present in *Palaeolagus*, is very faint in this genus. The incisive swelling extends back only beneath $M\overline{1}$, and is therefore proportionately shorter than in *Palaeolagus*. In this character, therefore, *Megalagus* is more specialized than *Palaeolagus* if Burke is correct that there is progressive reduction of the lower incisor among early leporids. The symphysis is massive, consisting of two or three interlocking ridges, as in Recent leporids, but heavier than is usual in the modern genera.

The *upper incisors* appear to be unknown.

"The superior molars are similar in general to those of the *P. haydeni*, but in none of them do I observe the fissure of the inner side of the crown. In several of them the median crescent persists, so that if the internal fissure exist at any time it must be speedily removed by attrition. In *P. haydeni* it remains after the disappearance of the crest, as in that species there is no enamel on the external side of the crown." (Cope, 1884, p. 883.) In all the upper cheek teeth except $P\underline{2}$ and $M\underline{3}$, the buccal part of the crown is supported by well developed, though rather slender, roots. Cement is present to a very limited extent, or is even entirely absent.

$P\underline{2}$ in general resembles the same tooth of *Palaeolagus*. The buccal lobe, however, is considerably more reduced even than in *Palaeolagus* (Fig. 106). As in *Palaeolagus*, the lingual lobe tends progressively to increase in size at the expense of the rest of the tooth. There appears to be considerable variation in the size of this tooth even within the single

species *M. brachyodon*. This suggests the likelihood that this tooth is undergoing the initial stages of a rapid reduction in that species, especially as the lingual lobe is less reduced than in *Mytonolagus* (Burke, 1934, p. 402). There appears to be only a single root supporting this tooth.

P$\underline{3}$ is much more primitive than the corresponding tooth of *Palaeolagus*, and is rather similar to that of *Desmatolagus*. The lingual lobe is much less developed than in *Palaeolagus*. In *Megalagus*, the anterior end of this lobe has turned buccad, and extends half way across the tooth, just separating the central lobe from P$\underline{2}$ (Figs. 100 and 106). This is an even more primitive stage than in some specimens of *Mytonolagus* (Burke, 1934, Pl. L, Fig. 1), and is only slightly further specialized than dP$\underline{2}$ of *Palaeolagus* (see above, Fig. 81). The possible significance of the variation of this tooth in *Mytonolagus* has been discussed above (page 290). The central lobe arises near the buccal part of the tooth, and extends linguad, instead of anterad as in *Palaeolagus*. It seems reasonable to believe that this is the more primitive condition. The buccal lobe is very small and poorly developed, again closely resembling that of dP$\underline{2}$ in *Palaeolagus*. There is no trace of the accessory lobules seen in P$\underline{3}$ of that form, except for a small crest beginning to extend along the buccal side of the tooth. This tooth is much less molariform in shape than the corresponding tooth of *Palaeolagus*. The anterior half of the tooth, in particular, is much narrower than the posterior, whereas in *Palaeolagus*, they are of nearly equal width. The valley between the central and lingual crests is open anteriorly for most of the animal's life, whereas in *Palaeolagus* this valley closes early in life. The valley, of course, opens on the anterior side of the tooth in *Megalagus* and on the buccal side in *Palaeolagus*, due to the extensive buccad growth of the lingual lobe in the latter genus. The hypostria is very much smaller in *Megalagus* than in *Palaeolagus*. From the few available specimens, it would appear certain that this valley is never more than a faint groove on P$\underline{3}$ of this genus.

P$\underline{4}$ is essentially molariform. When compared with the corresponding tooth of *Palaeolagus*, a number of important differences appear. The valley between the buccal and central lobes is much deeper and more persistent than in *Palaeolagus*, and the hypostria is very much weaker. The buccal valley lasts for some time after the hypostria has been reduced to a faint groove on the lingual margin of the crown (Fig. 106). In *Palaeolagus*, of course, the reverse holds true. None of the premolars of *Megalagus* appears to be completely molariform since the hypostria is so weakly developed in these teeth. The buccal lobe is very much simpler than in *Palaeolagus*, there appearing to be none of the lobules so characteristic of that genus. This absence of lobules on the buccal lobe seems to be one of the diagnostic characters of *Megalagus*. The buccal barrier of the buccal fossa does not appear to be an outgrowth of the buccal lobe as in *Palaeolagus*, but to be an independent development. This tooth agrees with that of *Mytonolagus* in the persistence of the buccal fossa and in the very small size of the hypostria. Burke's figures of *Mytonolagus* show that in the unerupted premolars (Burke, 1934, Pl. L, Fig. 5), in the slightly worn tooth (op. cit., Pl. L, Fig. 10), and in the highly worn one (op. cit., Pl. L, Fig. 1), there is never any trace of a deep hypostria in either P$\underline{3}$ or P$\underline{4}$. Although no unworn specimens of the premolar series of *Megalagus* are at hand, the tooth pattern appears to agree very closely with that of *Mytonolagus*, both being in sharp contrast to the pattern found in *Palaeolagus*. That is, in *Megalagus*, the "protocone" and "hypocone" are not separated as distinct cusps, being merely parts of the lingual wall of the tooth separated by a faint groove, whereas, in unworn *Palaeolagus* teeth, they appear to be definite cusps.

No upper deciduous teeth of *Megalagus* have been seen.

The *molars* are more like those of *Palaeolagus* than are the premolars. In M1–2, however, the buccal lobe is still small and simple, with no trace of the radiating lobules described in the discussion of *Palaeolagus*. Therefore, there is never any trace of the postero-buccal lake seen in that genus. The crescentic lake, representing the remnant of the valley between the lingual and central lobes, is nearer the buccal side of the tooth than in *Palaeolagus*, and retains its buccal exits longer than in that genus. In this it resembles *Desmatolagus*. These buccal openings are by no means as persistent as in the last genus, however, and the lingual end of the crescent is not as far linguad in *Megalagus*. Moreover, there does not appear to be any tendency for the subdivision of the crescent into two parts, as occurs in *Desmatolagus*. The buccal wall of the tooth is formed by what appears to be a backward growth from the anterior end of the central lobe, rather than by an anterad growth of the buccal lobe, as in *Palaeolagus*. The lingual lobe forms an even larger proportion of the tooth than in *Palaeolagus*. No unworn or slightly worn upper molars of *Megalagus* have been seen, but the hypostria certainly extended into the posterior part of the tooth as in *Mytonolagus* (Fig. 106). As in that genus, and in sharp contrast to the conditions in *Palaeolagus*, only a small amount of wear is needed to separate the buccal part of the hypostria as a lake, elongate at first, but rapidly reduced to an almost circular outline. When this happens, the hypostria remains only as a faint groove on the lingual surface of the tooth (Fig. 100). This is one of the major differences between the *Palaeolagus-Archaeolagus-Hypolagus-Lepus* group on the one hand, and the *Mytonolagus-Megalagus-Desmatolagus* group, on the other.

M3 is fairly large for a lagomorph, and the pattern can be seen with reasonable clarity (Fig. 100). This tooth appears to have a pattern suggestive of that of the other molars, reduction not having proceeded as far as in either *Palaeolagus* or *Desmatolagus*.

As the upper teeth are worn, the limit of deposition of the enamel on the buccal side is soon reached. When this occurs, the rate of wear naturally is increased. The extreme antero-buccal and postero-buccal corners of the teeth are rendered more resistant by the fact that they are supported by the roots. Therefore, wear causes the development of a median buccal notch in the outline of the tooth, and two others, on the anterior and posterior sides of the tooth, respectively, just linguad of the roots. When this takes place, the tooth has the general shape of a flatworm. Further wear results in the deepening of these notches, until finally they unite, and the tooth is separated into three parts, two supported by the buccal rootlets and the third by the main lingual root. The further modification of the last proceeds in the same manner as in *Palaeolagus*. The portions supported by the rootlets rapidly disappear. As in *Mytonolagus*, M1 is the widest tooth, but is not as much wider than the others as in that form. The teeth are sufficiently high crowned so that they protrude into the orbit.

"The inferior incisor is not deeper than wide, and is obtuse behind. The anterior face is nearly plane, and the enamel is marked by numerous approximated, faint transverse undulations in well preserved specimens" (Cope, 1884, pp. 883–884).

The pattern of P3 is one of the most easily recognized diagnostic features of this genus, having been noted by Cope in the original description of *M. turgidus* (1873*c*). Although, after slight wear, the tooth develops a pattern fundamentally similar to that of *Palaeolagus*, in the unworn stage there appear to be certain important differences. The

least worn specimen of the genus that I have seen is the holotype of *Palaeolagus triplex* (Fig. 102), which is undoubtedly merely a juvenile *M. turgidus*. The crown is more compressed antero-posteriorly than in *Palaeolagus*. The trigonid is composed of two cusps, uniting in a backwardly pointing V in the center of the tooth, as in *Palaeolagus*. The difference in the pattern is caused by the fact that the metaconid has been rotated backward, so that, instead of the protoconid and metaconid reaching forward to the same level, as in *Palaeolagus*, the protoconid is much farther forward in *Megalagus*. As a result, the crest from the protoconid runs antero-posteriorly, and that from the metaconid nearly transversely. In *Palaeolagus*, these two crests diverge approximately an equal amount from the antero-posterior axis of the tooth. This posterior rotation of the metaconid brings it very close to the entoconid, which has moved slightly forward, so that even in unworn teeth, these two cusps are nearly united. As a result, the first point where the dentine prisms of the talonid and trigonid unite is between the metaconid and the entoconid. Hence, the lingual fold in worn specimens of this tooth is only a faint groove, instead of being a deep fold as in *Palaeolagus*. That is, the portion of the valley in *Megalagus* homologous to the buccal part of the lingual fold of *Palaeolagus* is never part of the lingual fold of the former genus, but drains buccad into the buccal fold. Although the trigonid and talonid eventually unite in the center of the tooth, as they do in *Palaeolagus*, the portion of the buccal valley linguad of this point disappears before the two lobes unite in the center, so that there is never any lake in this part of the tooth. Except for the anterad curve of the entoconid and the antero-posterior compression, the talonid is essentially the same as that of *Palaeolagus*. The posterolophid, however, is quite small and is much lower than the rest of the talonid. Worn specimens rapidly develop the characteristic *Megalagus* pattern (Figs. 103, 104 and 110), similar to that of aged specimens of *Palaeolagus*, but attained very much earlier in life. This pattern in *Megalagus* is acquired at a time when the enamel is complete around the entire tooth, whereas in *Palaeolagus* the lingual enamel disappears before this pattern is reached. With further wear in *Megalagus*, the valley gradually shoals, and eventually has essentially disappeared. The enamel appears to have been deposited to a uniform distance all around the tooth, so that interruptions of the enamel are rare.

$P\overline{4}$ seems to differ very slightly from the corresponding tooth of *Palaeolagus*, except that the posterolophid lobule is slightly smaller in *Megalagus*. As far as can be told from the few available specimens, the crown pattern of *Megalagus* closely resembles that of *Palaeolagus*. The talonid and trigonid appear to unite slightly earlier in life than they do in *Palaeolagus*.

The anterior molars, like $P\overline{4}$, agree essentially with those of *Palaeolagus*. The most important differences are the larger size of *Megalagus*, and the fact that the teeth are shorter crowned than in *Palaeolagus*.

$M\overline{3}$ is rather different from that of *Palaeolagus*. The trigonid is very similar in the two genera, but the talonid of this tooth in *Megalagus* is much reduced, and appears to consist of but a single cusp in the center of the posterior side of the tooth.

The milk teeth (Fig. 101) appear to be identical in pattern with those of *Palaeolagus*, but, as in the case of all the other teeth, to have much smaller amounts of cement than do the teeth of the latter genus.

The enamel extends well down on the posterior side of the lower molars, and is ex-

tremely limited on the anterior face of these teeth. Laterally and internally, however, it forms a more nearly level line. It takes but little wear to destroy the enamel on the anterior face of the lower molariform teeth. There are two roots, one under the talonid and one under the trigonid. The teeth are long in proportion to their width, though not as much so as in *Mytonolagus*. This is a primitive character. The roots of the teeth are long, reaching nearly to the lower border of the mandible, as in *Lepus*. The lingual ends of the trigonids are not produced as in *Lepus*, ending more nearly squarely as in *Mytonolagus*.

The worn pattern of $P\bar{3}$ of *Megalagus* suggests that this genus is related to *Archaeolagus* and through it, perhaps, to *Hypolagus* and *Lepus*. The details of the pattern of $P\bar{3}$, and the small size and transient nature of the hypostria of the upper teeth, however, show that this genus cannot be closely related to any known later genera. *Archaeolagus ennisianus* shows only a single groove on the anterior face of $P\underline{2}$ (Dice, 1917, Fig. 1). The reduction of the outer lobe in $P\underline{2}$ of *Megalagus brachyodon* suggests the initial stage in such a direction, although I do not know that this tooth in *Archaeolagus* has attained its pattern in this manner. *Mytonolagus* does not show such a reduction, which is an indication of the primitive character of that genus.

*Megalagus* runs throughout the Lower and Middle Oligocene, paralleling its contemporaneous *Palaeolagus*. It is very much larger than the latter, the two standing in about the same size relationship as do the jackrabbit and the cottontail at present. In the White River, however, the larger genus was the more primitive, at least in its skull and dentition, the reverse of the relationship at the present time.

The skeleton of *Megalagus* is known only from fragments. Only the proximal and distal ends of the *humerus* are preserved. The bicipital groove is much deeper than in *Palaeolagus*, and the posterior side of the deltoid crest is more marked than in that form. "The distal portion of the *humerus* has a greater transverse extent than that of the *P. haydeni*, chiefly because of the greater size of the internal epicondyle. The external trochlea of the condyles extends also a little farther outwards beyond the external posterior trochlear flange. The corresponding internal flange is not nearly so prominent as in *P. haydeni*. The olecranar fossa is scarcely perforate; the coronoid fossa is shallow. The external marginal acute edge is prolonged well upwards" (Cope, 1884, p. 884).

The *ulna* is represented only by an olecranon. This is much more like that of *Lepus* than is that of *Palaeolagus*. It is, however, rotated mesially as in the latter genus. The keel below the semilunar notch is almost as small as in *Lepus*. The groove for the triceps is as deep as, or deeper than, in *Lepus*, being quite different from conditions in *Palaeolagus* in this respect. In general, the ulna of this form is much more progressive than in its contemporary *Palaeolagus*, and suggests a skeleton more specialized in a cursorial direction.

The *pelvis* is represented by some fragments in the American Museum collections. These approach much nearer the modern leporids than does the pelvis of *Palaeolagus* in the size and shape of the tubercle and in the fact that the tubercle is no longer on a high pinnacle. It still more nearly resembles the tubercle of *Palaeolagus* in this respect than it does that of *Lepus*, but it shows progress toward the latter type.

The proximal end of the *femur* has approximately the same form as that of *Palaeolagus*, the third and lesser trochanters not yet having expanded into a flattened plate. The former has, however, moved up the shaft until it is opposite the lesser trochanter. The intertrochanteric fossa is deeper proportionately than in *Palaeolagus*. The lesser trochanter

is much higher than in *Lepus*. The distal end of the bone does not appear to differ from that of *Palaeolagus*, except in its larger size. The femur is not flattened on the posterior side as is that of *Lepus*, agreeing in this with that of *Palaeolagus*.

The distal portion of the *tibio-fibula* is very large and massive. It is flattened anteroposteriorly but is very broad. The fibula is completely fused with the tibia at this end, only a very faint trace of their former point of separation being visible. The external and internal malleoli are strong and the facets for the astragalus and calcaneum are large and prominent. The keels are distinctly higher than in *Palaeolagus*. The fibular epicondyle is not hooked as in *Palaeolagus*, agreeing in this with *Sylvilagus* and *Lepus*. The calcaneal articulation is oval as in *Sylvilagus*, rather than crescentic as in *Palaeolagus*. A faint ridge blocks the anterior margin of the groove for the mesial keel of the astragalus. This is the first step in the development of the conditions seen in *Sylvilagus* and *Lepus*. The fossa for the lateral keel is weak and parallel to that for the mesial keel of the astragalus, as in *Palaeolagus* and in contradistinction to *Sylvilagus* and *Lepus*.

The *calcaneum* is more like that of *Palaeolagus* than like those of later forms. The *tuber calcis* is very faintly grooved for the tendon of Achilles, being rather similar in this respect to *Hypolagus*. The rugosity for the *flexor digitorum* is more pronounced than in *Palaeolagus*, and is, in fact, a well marked crest, indicating more powerful flexors of the toes than in *Palaeolagus*. The facet for the fibula is like that in *Palaeolagus*. The astragalar foramen is similar to that in *Palaeolagus* in position and relationships. The ectal facet is like that of *Palaeolagus*, rather than like that of the Recent forms. There definitely appears, however, to have been no possibility of motion between the astragalus and calcaneum, due to the interlocking of the distal ends of the bones, the hook on the end of the astragalus fitting into a slot in the distal end of the calcaneum. The distal ends of the two bones form a transverse line, agreeing in this respect with *Palaeolagus*. In Recent leporids, on the other hand, there is a marked calcaneo-navicular contact. There is no trace of the raised process for the articulation with the astragalus, seen on the calcaneum of *Palaeolagus*. The cuboid facet shows the first stages in the development of the L-shape seen in Recent leporids. The distal end of the bone is otherwise identical with that of *Palaeolagus*.

The *astragalus* has the same general shape as that of *Palaeolagus*. The divergence of the distal end from the axis of the keels is about as in *Sylvilagus*, though the distal end curves medially slightly more than in that form. The keels are like those of *Palaeolagus*. The tibial keel just shows on the plantar surface, indicating greater power of extension of the pes than in *Palaeolagus*, though less than in modern forms. The ental facet is like that of *Palaeolagus*. The groove between the ectal and ental facets is very deep. Otherwise, this bone is like that in *Palaeolagus* and Recent genera.

The rest of the pes appears to be entirely unknown.

From what is known of the skeleton, it appears that, in this portion of its anatomy, *Megalagus* is considerably more advanced than is *Palaeolagus*. The keels on the bones are better developed, the union of the bones appears to be firmer, and the areas affected by the muscles indicate that these were proportionately stronger and contracted more rapidly. On the basis of a study of the skeleton and muscle attachments, it was concluded above that *Palaeolagus* was in approximately the same stage of locomotive evolution as *Ochotona*. On the same basis, *Megalagus* would seem to have been in approximately the

same stage as *Sylvilagus*. This emphasizes the point raised above, that *Megalagus* would seem to have occupied the same ecologic niche as the modern jackrabbits, and *Palaeolagus* that of the cottontails, since the jackrabbits are the better runners at present. The stage of dental evolution achieved by *Megalagus* would seem to rule it out from consideration as an ancestor of *Archaeolagus* and *Hypolagus*, a requisite more nearly filled by *Palaeolagus*. It is, of course, very probable that no known species of *Palaeolagus* was ancestral to the few Lower Miocene forms of which anything is known. *Megalagus* would appear to be a genus that was persistently primitive in many of its dental characters, and which specialized in a slightly aberrant dental direction, but which early began to evolve along the same skeletal line as that subsequently followed by the dentally more progressive leporids. It is probable that the primitive nature of the tooth pattern was a handicap that could not be overcome when the more progressive lines overtook *Megalagus* in skeletal evolution, and that as an outcome of the resulting competition, the *Megalagus* line became extinct. It would seem reasonable to suppose, from the possible presence of *Megalagus* as late as the Lower Miocene (see above, p. 331), that this extinction took place at about that time. The increasing cursorial specialization of the leporids probably developed *pari passu* with the increasing aridity of the plains.

Matthew (1903, p. 217) recognized that the species *brachyodon* and *turgidus* were more closely related to each other than to the other Oligocene leporids. Burke (1934) showed that *Mytonolagus*, *Megalagus brachyodon* and *M. turgidus* form a natural group, perhaps an ascending evolutionary series, but that at any rate *Mytonolagus* was much closer to *Megalagus* than to *Palaeolagus*. I find myself unable to agree completely with Burke (op. cit., p. 414) in classing *Palaeolagus intermedius* in this series (see above, p. 329). It is quite possible that some at least of the material referred to the last named species really belongs in *Megalagus*, but I can not separate the holotype from *Palaeolagus*.

No illustrations of the skeleton of *Megalagus* have been included in this article, since the material is so extremely fragmentary and since the differences from the corresponding portions of *Palaeolagus* are so small that it would be difficult adequately to indicate them in figures of the fragments that are preserved. Most of the known specimens have already been figured by Cope (1884, Pl. LXVII, Figs. 21–27).

### **Megalagus turgidus** (Cope)

*Palaeolagus turgidus* Cope, Palaeontological Bulletin No. 16, 1873.
*Palaeolagus triplex* Cope 1873*c*.
*Tricium paniense* Cope 1873*c*.
*Megalagus turgidus* (Cope), Walker 1931*b*.

Figs. 100–105; Cope, 1884, Plate LXVII, Figs. 13–28

*Holotype:* Amer. Mus. Nat. Hist. No. 5635.

This species is rather rare in the Brulé. It can readily be told from all other known leporids of that age by its larger size. The teeth are hypsodont, but are still much lower crowned than are those of *Palaeolagus*. Roots are present on the buccal sides of the upper teeth, and perform a relatively important part of the support of the crown. This species may be told from *M. brachyodon*, the only other known member of the genus, by its greater hypsodonty.

Cope (1885, p. 163; 1889, p. 151; 1891, p. 5) and Lambe (1908, p. 58) both mention this form in the material from the Cypress Hills. If any member of the genus occurred there, it would probably be *M. brachyodon*, but so far, although I have examined all the material in the Canadian National Museum and in my own collections, I have seen nothing

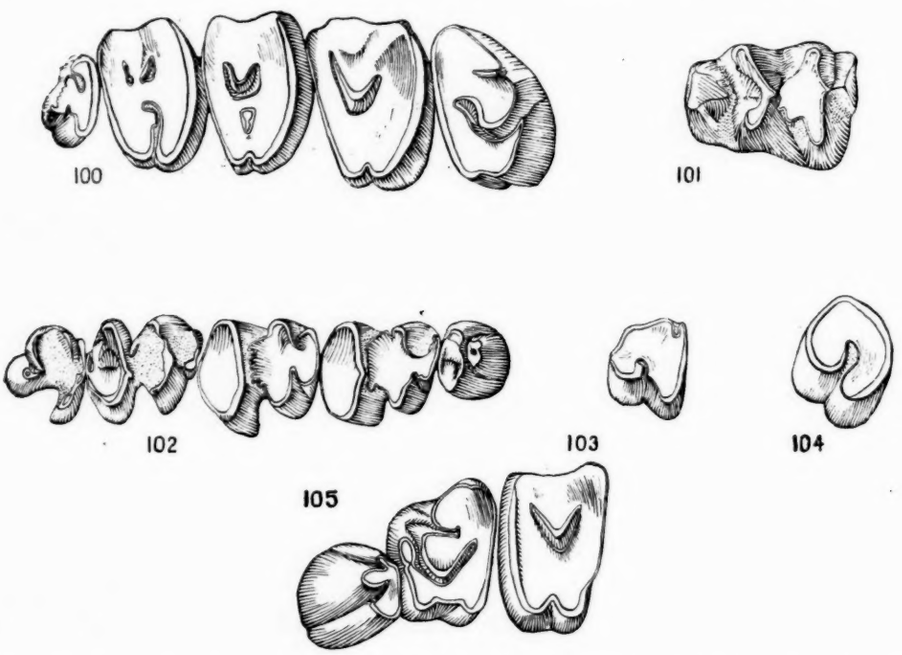



Fig. 100. *Megalagus turgidus*. Amer. Mus. Nat. Hist. No. 5632. P3–M3 right. Anterior end to the right.
Fig. 101. *M. turgidus*. Paul McGrew No. 101. dP3 left.
Fig. 102. *M. turgidus*. Amer. Mus. Nat. Hist. No. 5630, holotype of *Palaeolagus triplex*. P3–M3 left.
Fig. 103. *M. turgidus*. Amer. Mus. Nat. Hist. No. 5644, P4 left.
Fig. 104. *M. turgidus*. Amer. Mus. Nat. Hist. No. 5651. P3 left.
Fig. 105. *M. turgidus*. Amer. Mus. Nat. Hist. No. 12,286. P2–4 left.
All figures × 5 except Fig. 101, which is × 7.5.

which suggests this genus in the slightest degree. Cope describes the material as being *P. turgidus*, and as consisting of "mandibular rami identical in character with those from the White River beds of Dakota and Colorado." (Cope, 1891, p. 5.) It seems very probable that Cope had some specimens of *M. brachyodon* which have since been lost.

*Palaeolagus triplex* Cope is unquestionably merely a specimen of *M. turgidus* with the unworn permanent dentition (see Fig. 102). In his earlier reports, Cope erected the genus *Tricium* and several species, some of which he later referred to *Palaeolagus*, on the basis of the deciduous dentition. In his great monograph, he recognized that *Tricium* was merely a stage of wear of *P. haydeni* (1884, p. 877), and that *P. agapetillus* was a slightly later stage in the same wear series (op. cit., pp. 877–878), but did not recognize that *P. triplex* was merely the same stage of wear as *P. agapetillus*. His description of *P. triplex* is given below. "This rabbit is known from a single incomplete left mandibular ramus,

which supports all the molar teeth in perfect preservation. It belonged to an adult animal, but the first inferior molar [= P$\bar{3}$] is but little worn, showing that the individual had but just attained maturity. This species is larger than the *Palaeolagus haydeni*, and is equal in size to the *P. turgidus*. It differs materially from both species in the constitution of its molar teeth. The first molar [= P$\bar{3}$] is peculiar in having an anterior as well as an external groove, the result being a trilobate instead of a bilobate section. This character would be maintained during the life of the animal, as the groove continues well into the alveolus [It does not reach far into the alveolus, however]. The four intermediate molars are characterized by the presence of a third column posterior to the second, and of smaller diameter. It is at first isolated from the second by enamel investment, but on wearing becomes connected with it. They remain distinct to an advanced age of the animal, since the grooves which bound them descend far into the alveoli before disappearing. Another characteristic of the specimen at least, is seen in the intervention of a wide isthmus between the two principal lobes of each molar, or, in other words, of a narrowed portion of the second column between its transverse portion and the anterior column. The result is that the triturating surfaces of the posterior column of the molar has a quadrilobate outline; one lobe anterior, one posterior, and two lateral. The tuberosity of the inner side of the ramus, which incloses the incisive alveolus, extends to below the second molar. Its surface, and a portion of that above it, is roughened with small punctiform impressions. The external face of the ramus is smooth and somewhat convex anteroposteriorly and vertically. The anterior border of the masseteric fossa is not prominent, as in *P. turgidus*, is regularly convex, and extends to the line of the posterior border of the penultimate molar. This species rests on characters which I have observed to be transitional in the *P. haydeni*, and I have attended to the possibility of the individual which has furnished them being a similarly immature *P. turgidus*. In a considerable number of specimens of the latter no approach to the present one is exhibited; the latter is a fully-grown animal, and its characters would remain after long attrition of the teeth" (Cope, 1884, pp. 881–882).

I believe that the reason Cope did not find any intermediates between the type and only specimen of *P. triplex* and his material of *P. turgidus* is that the others (with the exception of the holotype of *Tricium paniense*, which consists of dP$\bar{3}$–$\bar{4}$) are all fully adult, and that *Megalagus* is distinctly rarer than *Palaeolagus*. All of the characters listed as distinctive of *P. triplex* are those of a juvenile individual. Although Cope was correct in stating that the pattern remains fundamentally unchanged as far as the alveoli, nevertheless there is a distinct decrease in the depths of the accessory folds, and the teeth at the alveolar border are distinctly nearer the pattern of *Megalagus turgidus* than they are at the wear surface. In view of the extremely rapid wear in leporid cheek teeth, and of the great distance from the unworn crown to the roots (which are never present at the same time in Middle Oligocene forms), it is apparent that there would be ample time during the life of an individual for all traces of the "*triplex*" pattern to be destroyed, leaving that of *M. turgidus*. The relationships of *P. triplex* and *M. turgidus* are exactly the same as those of *Protolagus affinus* and *Palaeolagus haydeni*, as discussed above (page 300).

*Megalagus turgidus*

MEASUREMENTS OF CHEEK TEETH IN MILLIMETERS

| | *Amer. Mus. Nat. Hist. No. 5632* | *Amer. Mus. Nat. Hist. No. 12,268a* | *A.E.W. No. 9237* |
|---|---|---|---|
| P2 antero-posterior | | 1.12 | |
| width | | 1.82 | |
| P3 antero-posterior | 2.58 | 2.58 | 2.16 |
| width protoloph | 3.48 | 2.85 | 4.15 |
| width metaloph | 4.30 | 3.83 | 4.32 |
| P4 antero-posterior | 3.02 | 2.80 | 2.44 |
| width protoloph | 4.37 | 3.92 | 4.40 |
| width metaloph | 4.58 | 4.34 | 4.40 |
| M1 antero-posterior | 2.64 | | 2.23 |
| width protoloph | 4.28 | | 4.12 |
| width metaloph | 4.25 | | 4.25 |
| M2 antero-posterior | 2.72 | | 2.02 |
| width protoloph | 4.10 | | 3.84 |
| width metaloph | 4.03 | | 3.26 |
| M3 antero-posterior | 1.37 | | 0.90 |
| width | 2.18 | | 2.58 |

| | *Amer. Mus. Nat. Hist. No. 5630, holotype of Palaeolagus triplex* |
|---|---|
| P3 antero-posterior | 1.76 |
| width trigonid | 1.20 |
| width talonid | 2.14 |
| P4 antero-posterior | 3.28 |
| width trigonid | 2.40 |
| width talonid | 2.10 |
| M1 antero-posterior | 3.42 |
| width trigonid | 2.80 |
| width talonid | 2.45 |
| M2 antero-posterior | 3.27 |
| width trigonid | 2.74 |
| width talonid | 2.25 |
| M3 antero-posterior | 1.29 |
| width trigonid | 1.73 |
| width talonid | 0.90 |

*Range:* Middle and probably Upper Oligocene of the Great Plains States.

**Megalagus brachyodon** Matthew

*Palaeolagus brachyodon* Matthew, Bull. Amer. Mus. Nat. Hist., Vol. XIX, 1903.
*Palaeolagus turgidus* Cope 1885.
*Palaeolagus ?turgidus* Cope, Douglass 1901.
*P. ?triplex* Cope, Douglass 1901.
*Megalagus brachyodon* (Matthew), Burke 1936.

Figs. 106–110

*Holotype:* Amer. Mus. Nat. Hist. No. 9652.

This species is one of the shortest crowned of all the rabbits, being second only to *Mytonolagus petersoni*. When the teeth are first erupted, the roots are barely, if at all, developed, and the crown is at least 8 mm. long.

The upper teeth are distinctly shorter crowned than are the lowers, on the buccal side, but lingually they are just as hypsodont as the lower teeth. The material referable to this species is not very abundant, since many of the specimens that have been referred here turn out actually to belong to *Desmatolagus*. It is difficult always to be certain of the proper allocation of the lower teeth, but the upper teeth are simple to tell apart. There appear also to be a considerable number of specimens intermediate in size between *M. brachyodon* and *P. temnodon*, but not sufficient material is available at the present time to be certain on this point.

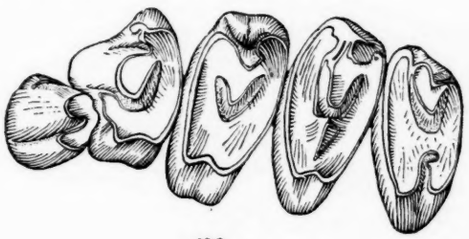

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Fig. 106. *Megalagus brachyodon*. Amer. Mus. Nat. Hist. No. 9652–9653. P$\underline{2}$–M$\underline{2}$ left.
Fig. 107. *M. brachyodon*. A. E. W. No. 9225. P$\underline{4}$ right.
Fig. 108. *M. brachyodon*. Amer. Mus. Nat. Hist. No. 8050. P$\bar{4}$–M$\bar{2}$ left.
Fig. 109. *M. brachyodon*. A. E. W. No. 9046*c*. M$\bar{1}$–2 left.
Fig. 110. *M. brachyodon*. A. E. W. No. 9046*i*. P$\bar{3}$ right.
All figures × 5.

*Megalagus brachyodon*

MEASUREMENTS OF CHEEK TEETH IN MILLIMETERS

| | *Holotype, Amer. Mus. Nat. Hist. No. 9652* | *A.E.W. No. 9225* |
|---|---|---|
| $P\frac{2}{2}$ antero-posterior | 2.40 | |
| width | 2.65 | |
| $P\frac{3}{3}$ antero-posterior | 2.45 | |
| width protoloph | 3.00 | |
| width metaloph | 3.78 | |
| $P\frac{4}{4}$ antero-posterior | 2.90 | 2.67 |
| width protoloph | 4.22 | 3.88 |
| width metaloph | 4.65 | 4.14 |
| $M\frac{1}{1}$ antero-posterior | 2.78 | |
| width protoloph | 4.74 | |
| width metaloph | 4.43 | |
| $M\frac{2}{2}$ antero-posterior | 2.39 | |
| width protoloph | 4.21 | |
| width metaloph | 3.70 | |

| | *Amer. Mus. Nat. Hist. No. 8050* | *A.E.W. No. 9046a* | *A.E.W. No. 9046c* |
|---|---|---|---|
| $P\frac{3}{3}$ antero-posterior | | 2.48 | |
| width trigonid | | 1.92 | |
| width talonid | | 2.52 | |
| $P\frac{4}{4}$ antero-posterior | 2.98 | | |
| width trigonid | 2.10 | | |
| width talonid | 1.95 | | |
| $M\frac{1}{1}$ antero-posterior | 3.00 | | 3.42 |
| width trigonid | 2.54 | | 3.18 |
| width talonid | 2.36 | | 2.60 |
| $M\frac{2}{2}$ antero-posterior | 3.19 | | 3.24 |
| width trigonid | 2.40 | | 3.03 |
| width talonid | 1.97 | | 2.48 |

*Horizon and Locality:* Lowest Oligocene of Pipestone Springs, Montana.

**Desmatolagus** Matthew and Granger

*Desmatolagus* Matthew and Granger, Amer. Mus. Novitates No. 102, 1923.

Figs. 111–113; Matthew and Granger, 1923, Figs. 10–12; and Burke, 1936, Figs. 6–7

*Genotype: Desmatolagus gobiensis* Matthew and Granger 1923.

Until the publication of Burke's fine paper, the American species of this genus were completely confused with those of *Megalagus*, one of the paratypes of *M. brachyodon* apparently belonging to this genus (Fig. 113). The most easily recognizable characters of this form are the persistent low crowns, the small size of $P\underline{2}$, $P\overline{3}$ and $M\frac{3}{3}$, the persistence of the buccal openings of the valleys in the upper molars throughout a large part of the animal's life, and the persistence of parts of the pattern for a long time.

*Range:* Oligocene of the Great Plains and Mongolia, and possibly of France.

Practically none of the skull or skeleton is known. The fragments of the palate and zygoma, in which cheek teeth have been found, seem very like those of *Megalagus*. The anterior end of the masseteric fossa ends in a knob below the rear of $M\overline{2}$, which knob is much more prominent than in *Megalagus*.

$P\underline{3}$ does not differ greatly from that of the other Oligocene leporids in its make-up, though the anterior lobe is longer than in *Megalagus*, reaching nearly to the buccal margin, approximately as in *P. temnodon*. The buccal lobe, however, is rounded and globular, as in the former, rather than spread out along the entire buccal border, as in the latter. The central lobe extends well linguad, but this is probably a wear character. The lingual lobe seems longer in the material available for study than is indicated by Burke's figure. The posterior arm of the crescentic lake is long.

In $P\underline{4}$ the buccal cuspules are retained much longer than the internal fold, as in *Megalagus*, rather than vice versa, as in *Palaeolagus*. The median valley is not dammed bucally as in *Megalagus*. Otherwise, in the state of wear the available specimens are in, not many differences between these genera are apparent in this tooth. The crescent is J-shaped, having a long posterior arm, which frequently is connected with the buccal margin of the tooth, leaving a buccal exit from the valley, and separating the central lobe from the buccal one. This suggests that the pattern of the posterior premolars of *Desmatolagus* may be quite different from that in the other two genera, although this arm of the crescentic lake may have secondarily grown buccad. The central lobe, which in *Palaeolagus* has been considered as perhaps being formed of the paracone and metacone, looks in *Desmatolagus* more like the metacone or the metacone plus the mesostyle, which would mean that the anterior marginal crest would then have to be formed of the paracone or the paracone plus the parastyle. It does not seem likely that the central of the three buccal crests of *Desmatolagus* (Figs. 111–112) is formed by the metacone at its internal end and of the paracone at its buccal, but, if the interpretations given elsewhere (pp. 351–356) are correct for *Palaeolagus*, this would have to be the case, unless it should be established that *Desmatolagus* has a tooth pattern fundamentally different from that of *Palaeolagus* and *Megalagus*, and hence an entirely separate ancestry, which seems extraordinarily improbable. The peculiar tooth pattern of this genus certainly throws doubt on the homologies attempted in this paper, but other evidence makes any other homologies

equally difficult to accept. It is therefore thought best to leave the section on cusp homologies as it is, and to admit that it is entirely hypothetical.

In M$\underline{1}$ the lingual valley disappears rapidly, as in *Megalagus* and in contrast to conditions in *Palaeolagus*. An oval lake is left, as in the other leporids. This tooth resembles the premolars of *Palaeolagus*. There are two folds from the buccal margin, which would unite in the center of the tooth to form a crescent, in the right stage of wear. No teeth in this stage have been seen, all the specimens that I have encountered showing the crescent divided into two nearly parallel lakes, due to the fact that the valley of the crescent is much shallower at its apex than on either arm. The posterior valley is divided into two parts by a slight warping of its floor about its middle.

M$\underline{2}$ has a pattern similar to that of M$\underline{1}$. In shape, it is much more like P$\underline{3}$ (Fig. 111), distinctly more so than is shown by Burke's figures, although other specimens (Fig. 112) show a more normal shape. The crown of the specimen in Figure 111 is subtriangular, M$\underline{3}$ having squeezed into the posterior angle. This does not seem to have been the case with any of the previously described specimens of *Desmatolagus*. Toward the root, this condition is exaggerated, so that the basal view of the tooth is L-shaped, M$\underline{3}$ fitting into the angle between the arms of the L. The rear of the tooth is definitely grooved for the admission of M$\underline{3}$. The two arms of the central crescent lake are still open bucally in this specimen.

As Burke pointed out, M$\underline{3}$ is greatly reduced in size. However, in addition, it is also more reduced in pattern than the corresponding tooth of other Oligocene leporids. It does not show the bilophodont pattern of *Palaeolagus*, but has an anterior loph which gives off several posterior lobules, so that the tooth is approximately a mirror image of P$\underline{2}$. Although some authors might draw conclusions of great phylogenetic significance from this resemblance, I do not believe that it indicates anything more than that the mechanical stresses at the two ends of the cheek tooth series are similar.

One characteristic of this form is the great transverse elongation of the upper cheek teeth with wear. All of the "*Megalagus*" upper teeth that are very wide transversely turn out actually to be those of *Desmatolagus*. Since this form has as low a crown buccally as does *Megalagus*, the elongation is due to increased rapidity of lingual growth, so that the tooth pivots around the buccal roots. As a result, the wear surface becomes more and more oblique to the long axis of the tooth, and correspondingly increases in area with advancing age. This rotational growth appears to be a distinctive character of *Desmatolagus* as opposed to all other leporids with which I am familiar. It might be considered to be an analogy to the rotation of the teeth of *Heliocoprion*.

From the available material, it is almost impossible to make any statements about the lower cheek teeth except that P$\overline{3}$ and M$\overline{3}$ are reduced in size. If these teeth are present, the material can readily be separated from *Megalagus*. If they are not preserved, I do not know of any method of separating the lower teeth of these two genera.

Like *Megalagus*, *Desmatolagus* has a small amount of cement in the deeper folds of both upper and lower teeth, but a much smaller amount than exists in *Palaeolagus*.

The general evolutionary trends and relationships of *Desmatolagus* have been discussed by Burke in such a clear and thorough manner that I can not do better than to quote his conclusions on the subject.

"Species of *Desmatolagus* in the North American Oligocene may be distinguished from

contemporary species of *Megalagus* by their lower-crowned and more transverse cheek teeth, reduced $M\frac{3}{3}$ and somewhat simpler $P\underline{3}$. In the lower Oligocene the excess in size of $M\overline{2}$ over $M\overline{1}$ and $P\overline{4}$ may also prove characteristic of *Desmatolagus*, but at present I am not inclined to place much trust in this peculiarity. It may be anticipated that when the third lower premolars . . . are found they will also show more reduction and secondary simplification than in *Megalagus*, while $P\underline{2}$ may be expected to show more reduction also.

"While *Desmatolagus* in the lower Oligocene in general resembles *Megalagus*, the two genera do not keep apace in their later development. Middle and Upper Oligocene species of *Megalagus* strongly parallel *Palaeolagus* in the 'modernization' of their tooth structure. *Desmatolagus*, however, continues the reduction of $M\frac{3}{3}$ and if not the reduction, certainly the simplification of $P\overline{3}$; $P\underline{2}$ appears to be reduced and there are changes in the pattern of $P\underline{3}$ (this tooth also undergoes compression along its anterior face). There is some equalizing of the proportions of $P\underline{3}$–$\underline{4}$ and $M\underline{1}$–$\underline{2}$, perhaps better expressed as due to the increase in size of the premolars concerned. There seems to be, as regards the premolars at least, an increase in hypsodonty (Teilhard de Chardin even describes $P\frac{3}{3}$ of his *Desmatolagus pusillus* as of continuous growth). But it is noteworthy that *Desmatolagus* also preserves, in the Upper Oligocene, an assemblage of characters which are found in the Eocene *Mytonolagus* and also in specimens of *Megalagus* from the lower Oligocene—curved superior cheek tooth shafts, relatively poorly developed unilateral hypsodonty, transverse cheek teeth and persistence of the crown pattern with wear. Certain of the above characters have doubtless been interpreted by some authors as indicative of Ochotonid affinities of *Desmatolagus*. To my way of thinking they are merely retained primitive characters, indicative of the unprogressiveness of the genus as a whole" (Burke, 1936, pp. 150–151).

"From present evidence, *Desmatolagus* . . . appears to me to have far too many characteristics of the *Leporidae* to be ancestral to any *Ochotonidae* or to warrant their inclusion in the latter family.

"*Desmatolagus* is already specialized along the lines of the *Leporidae* in the pattern of its cheek teeth. Despite the marked persistence of the internal valley in $P\overline{4}$ and in the inferior molars (a condition which, by the way, can be found in certain species of *Palaeolagus*, even in the Upper Oligocene) these inferior cheek teeth are thoroughly leporine as regards their construction; they show the characteristic crowding of the paramere cusps and a main valley extending transversely across the tooth from the protomere which separates the trigonid from the talonid. In the *Ochotonidae* the paramere cusps are widely separated, and while both the internal and the external valleys appear to have conjoined to form the separation between the trigonid and the talonid, it is of note that the external valley is directed postero-internally, while the internal valley is directed antero-internally, becoming confluent with the external valley by cutting across the latter in advance of its postero-internal channel. The superior molars of *Desmatolagus* show a narrow internal notch or valley, such as characterizes the *Leporidae* generally, and the course of the valley is postero-external, or at the most transverse, not in advance of the 'crescent'; the external portion of the valley becomes isolated as an enamel island as in *Mytonolagus*, *Megalagus* and *Palaeolagus*. In the *Ochotonidae* the internal cusps of the molars are well separated

by a wide internal valley which is antero-externally directed, and which in the earlier forms is seen to be directed anterior to the 'crescent' " (Burke, 1936, p. 152). In all ochotonids that I have seen, the bases of the prisms of the cheek teeth pass into the zygoma, whereas in the leporids they extend into the orbit. It seems to me that a difference of this sort must be of primary significance, and that the common ancestor of the two families must have lived at a time when the upper cheek teeth were sufficiently low crowned so that their bases did not extend into either the orbit or the zygoma. Therefore, since *Desmatolagus* agrees with the leporids in this as well as in most other respects, I believe that it must assuredly be a member of the Leporidae, and that it certainly can not be referred to the Ochotonidae.

### **Desmatolagus dicei** Burke

*Desmatolagus dicei* Burke: Ann. Carn. Mus., Vol. XXV, 1936.

Figs. 111–113 and Burke, 1936, Fig. 6

*Holotype:* Carn. Mus. No. 814.

Burke defined this species as follows: "Species larger than *Desmatolagus robustus* . . .; premolars not as well developed, molars less reduced; external outlines of maxillary tooth row more evenly rounded; $M\overline{2}$ the largest inferior cheek tooth" (1936, pp. 149–150).

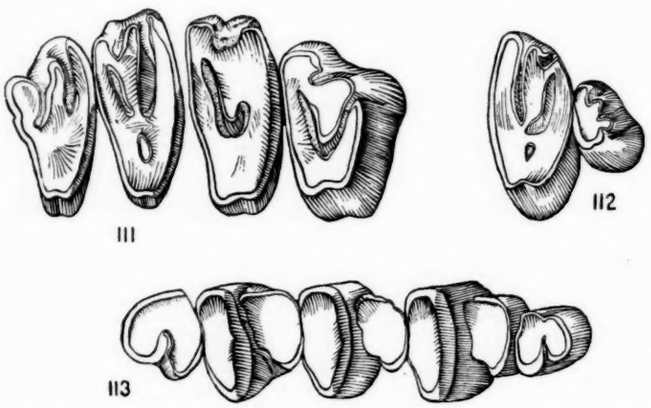



Fig. 111. *Desmatolagus dicei.* Amer. Mus. Nat. Hist. No. 9856. $P\underline{2}$–$M\underline{2}$ right.
Fig. 112. *D. dicei.* A. E. W. No. 9097. $M\underline{2}$–$\underline{3}$ left.
Fig. 113. cf. *D. dicei.* Amer. Mus. Nat. Hist. No. 9730. $P\overline{3}$–$M\overline{3}$ left.
All figures × 5.

This species is of about the same size as *Megalagus brachyodon.* Burke's measurements suggest a considerably larger animal than is indicated by the measurements given below. This may in part be due to differences in measuring, since there is no fixed point in lagomorph teeth from which everyone can take his measurements, or it may be due to a difference in the amount of wear, or it may actually be a difference in the size of the animals involved.

*Desmatolagus dicei*

MEASUREMENTS OF CHEEK TEETH IN MILLIMETERS

| | *A.E.W. No. 9097* | *Amer. Mus. Nat. Hist. No. 9856* |
|---|---|---|
| $P\frac{3}{3}$ antero-posterior | | 2.22 |
| width protoloph | | 3.18 |
| width metaloph | | 4.32 |
| $P\frac{4}{4}$ antero-posterior | | 2.58 |
| width protoloph | | 5.16 |
| width metaloph | | 5.39 |
| $M\frac{1}{1}$ antero-posterior | | 2.48 |
| width protoloph | | 5.32 |
| width metaloph | | 5.00 |
| $M\frac{2}{2}$ antero-posterior | 2.39 | 2.54 |
| width protoloph | 4.42 | 4.53 |
| width metaloph | 4.03 | 3.47 |
| $M\frac{3}{3}$ antero-posterior | 1.12 | |
| width protoloph | 1.91 | |
| width metaloph | 1.82 | |

| | *Amer. Mus. Nat. Hist. No. 9730* |
|---|---|
| $P\frac{3}{3}$ antero-posterior | 2.24 |
| width trigonid | 1.80 |
| width talonid | 2.41 |
| $P\frac{4}{4}$ antero-posterior | 2.96 |
| width trigonid | 3.20 |
| width talonid | 2.23 |
| $M\frac{1}{1}$ antero-posterior | 2.96 |
| width trigonid | 3.12 |
| width talonid | 2.13 |
| $M\frac{2}{2}$ antero-posterior | 2.88 |
| width trigonid | 3.11 |
| width talonid | 2.23 |
| $M\frac{3}{3}$ antero-posterior | 1.63 |
| width trigonid | 1.78 |
| width talonid | 1.31 |

*Horizon and Locality:* Lowest Oligocene of Pipestone Springs, Montana.

**Desmatolagus gazini** Burke

*Desmatolagus gazini* Burke: Ann. Carn. Mus., Vol. XXV, 1936.

Burke, 1936, Fig. 7

*Holotype:* Carnegie Mus. No. 37.

Burke defined this species as follows: "Species intermediate in size between *Desmatolagus gobiensis* . . . and *Desmatolagus robustus* . . .; external outline of maxillary tooth row less rounded than in *Desmatolagus dicei* . . . and premolar-molar proportions nearly as in *Desmatolagus robustus* . . . and *Desmatolagus gobiensis* . . ., but $P\underline{3}$ not as compressed along its anterior side and $M\underline{2}$ with unusually short posterior wall crest, external roots of superior cheek teeth stronger" (Burke, 1936, p. 150).

*Range:* Middle Oligocene of Sioux County, Nebraska.

?**Desmatolagus** sp.

*Palaeolagus* ? species, Wilson: Carnegie Institute of Washington Publ. No. 453, 1934.

Wilson describes this form as follows: ". . . the incisor apparently originates below $M\overline{1}$, as in *Palaeolagus*. The anterior edge of the masseteric muscle scar is situated beneath $M\overline{2}$. $P\overline{3}$ . . . . shows one strong external enamel inflection and lacks the small secondary external inflection characteristic of *Archaeolagus*. The presence or absence of this inflection may remain uncertain, in view of the preservation of the tooth, but the external wall possesses two ridges instead of three as found in *Archaeolagus*. The occlusal surface of the tooth exhibits a structure which may be regarded as an internal enamel inflection, but this is not at all certain. The internal wall of the tooth forms a shallow groove, extending partly down the side, and this may further suggest the presence of an inflection. However, the presence or absence of the internal enamel inflection can not be definitely established. . . . The enamel inflections of $P\overline{3}$ . . . occur at about the mid-point of the tooth, dividing it into two semi-circular lobes, the posterior one more elliptical, the anterior one apparently slightly drawn out at its anterior tip. The cheek-teeth $P\overline{4}$–$M\overline{2}$ show the posterior lobes joined to the anterior lobes at the buccal borders" (Wilson, 1934, pp. 16–17). There is very little more to be seen in Wilson's figures (Pl. 1, Figs. 4 and 4a) than he has indicated in the above description. Since the publication of his paper, Burke's study of *Desmatolagus* has appeared, which established the small size of $P\overline{3}$ and $M\frac{3}{3}$ as one of the characteristics of that genus. Since the Sespé specimen has a third premolar much smaller than its other teeth, it would seem reasonable to assign this form to *Desmatolagus*. This form also agrees with *D. dicei* in that $M\overline{2}$ is larger than $P\overline{4}$ and $M\overline{1}$, a feature which Burke hesitantly suggested as a character of the Lower Oligocene species.

*Horizon and Locality:* Upper Oligocene Sespé Beds of the Las Posas Hills, California.

**Archaeolagus** Dice

*Archaeolagus*, Dice: Univ. California Publ., Bull. Dept. Geol., Vol. 10, 1917.
*Genotype: Lepus ennisianus* Cope.

This genus comes typically from the John Day and Great Plains Lower Miocene. Certain authors, however, have cited this genus from the White River. Cook and Cook

(1933) mention it from the "Torrington area." The only specimens that have been described that could form the basis of this citation are those discussed by Schlaikjer (1935), who reports *A. ennisianus* from 200 feet above the Brulé-Harrison contact. As many of the references given by Cook and Cook are based on material in the Cook collection, it is entirely possible that they have some specimens of this genus from the Oligocene of the Torrington area.

Walker (1931*b*) described a specimen from the Brulé of central Wyoming as *Archaeolagus striatus*. As he published no figures, and as the description was somewhat vague, it was rather difficult to tell just what kind of an animal he was discussing. Walker stated that the holotype is an old individual, which suggested that it might merely be a much worn specimen of *Palaeolagus haydeni*, which does develop a pattern similar to that of *Archaeolagus*, and identical to that of *Megalagus*, when highly worn. Fortunately, Dice and Dice were able to study the holotype of Walker's species, and they published a figure of it (Dice and Dice, 1935, Fig. 23). They state: "The species *Archaeolagus striatus* Walker is based on a very old specimen, as is shown by the greatly worn teeth of the type. . . . None of the characters of the teeth of this specimen distinguish it from very old specimens of *Palaeolagus haydeni*, nor do there seem to be any characters of the skull which are distinctive. *Archaeolagus striatus* must, therefore, . . . be placed as a synonym of *Palaeolagus haydeni*" (Dice and Dice, 1935, p. 463).

Thus there are no forms as yet described from the White River that belong in *Archaeolagus*. With the fragmentary material which is usually preserved, and with only a superficial study of the extensive existing collections, it is impossible to state that *Archaeolagus* does not occur in the White River, since senescent individuals of *Palaeolagus* develop a tooth pattern close to that of younger individuals of *Archaeolagus*. It seems very probable, however, that *Archaeolagus* either did not live in the White River area during the Oligocene, or, if it did, that it was a rare form.

## DISCUSSION

As indicated above in the discussion of the cheek teeth of *Palaeolagus*, and as shown in the accompanying figures (Fig. 114), the cheek teeth of the leporids can be arranged in a series showing an almost complete gradation in all characters from the anterior premolars to the molars. This series is presented here with no desire to indicate relationships within the Leporidae, but to establish definitely the completeness of intergradation of pattern in this series, so as to establish the presumption that the corresponding parts of the teeth are homologous throughout the series. This would then serve as a basis for the interpretations of homologies with the cusps of normal mammals, discussed below. Whatever names may be applied to the parts of the teeth, it seems almost certain that the three lobes of $P\underline{2}$ are homologous to the similar parts of all the other premolars. This is one of the two principal points discussed by Ehik (1926). His interpretation of the relationships of the parts of the teeth is exactly that presented here. When I began this study, I had a strong feeling that Ehik's homologies between the different teeth were incorrect, largely because of a complete disagreement with his attempts at homologizing lagomorph cusps with those of other mammals. The completeness of my present agreement with his homologies within the order is perhaps an indication of the weight of evidence supporting his viewpoint. I do not, however, find myself in agreement with Ehik in the attempt at homology with other

mammals. Although I am not sure what the homologies of lagomorph cusps actually are, I believe that the rabbits are a more normal group of mammals than Ehik would make them. If his conclusions should prove to be correct, a logical deduction from them would be that the lagomorphs are not members of the Eutheria at all. Although this is a possibility, the present evidence seems overwhelming that the lagomorphs are merely somewhat atypical placentals.

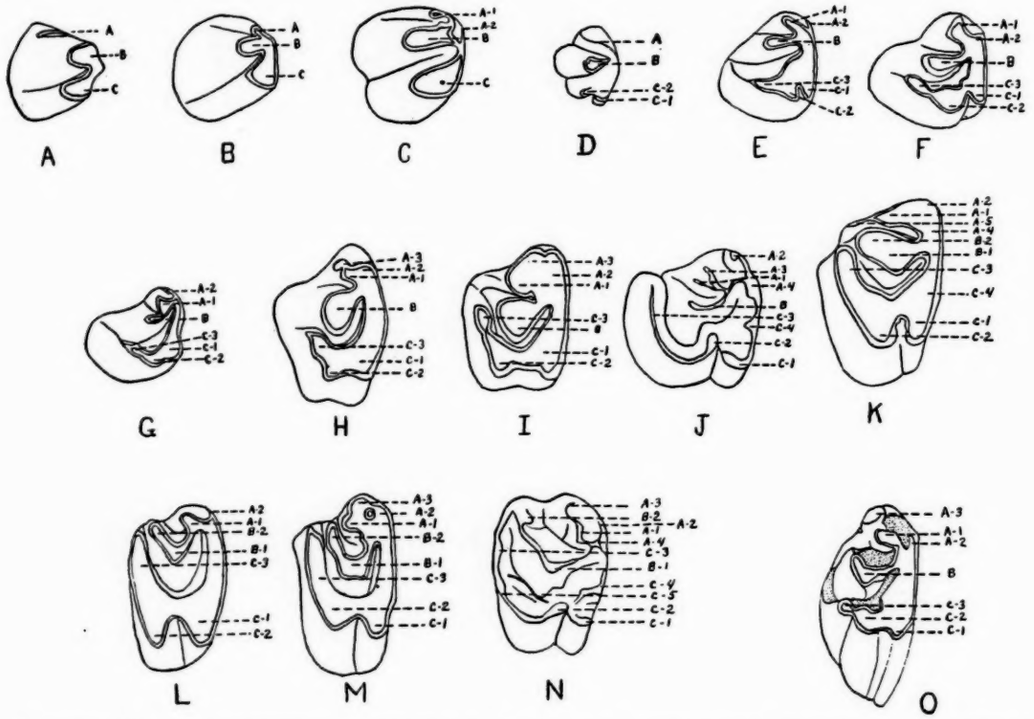



Fig. 114. Diagram of upper premolars and milk molars of lagomorphs, showing what appear to be the homologies.

A, B, and C, the three lobes discussed in the text.
1, 2, 3, etc., the lobules into which the lobes are divided.
A. $P\frac{2}{2}$, *Megalagus brachyodon* (Fig. 106).
B. $P\frac{2}{2}$, *M. turgidus* (Fig. 105).
C. $P\frac{2}{2}$, *Palaeolagus temnodon* (Fig. 79).
D. $P\frac{2}{2}$, *P. haydeni* (Fig. 71).
E. $dP\frac{2}{2}$, *P. temnodon* (Fig. 81).
F. $dP\frac{2}{2}$, *P. temnodon* (Fig. 82).
G. $dP\frac{2}{2}$, *P. haydeni* (Fig. 73).
H. $P\frac{3}{3}$, *M. brachyodon* (Fig. 106).
I. $P\frac{3}{3}$, *M. turgidus* (Fig. 105).
J. $P\frac{3}{3}$, *P. temnodon* (Fig. 80).
K. $P\frac{3}{3}$, *P. temnodon* (Fig. 79).
L. $dP\frac{3}{3}$, *P. temnodon* (Fig. 81).
M. $dP\frac{3}{3}$, *P. temnodon* (Fig. 82).
N. $P\frac{4}{4}$, *P. temnodon* (Fig. 80).
O. $P\frac{3}{3}$, *Titanomys fontannesi*, after Ehik.
Figures to various scales.

The problem of cusp homology between the members of this order and other mammals is quite difficult to solve. The tooth pattern of the earliest known lagomorphs is still so complex that it is difficult to reach a certain starting point. It is, for example, entirely uncertain whether the large central cusp (B-1, Fig. 115) is an amphicone, a metacone, or, as Burke has suggested, a paracone. Ehik considers it to be the protocone. On the basis of

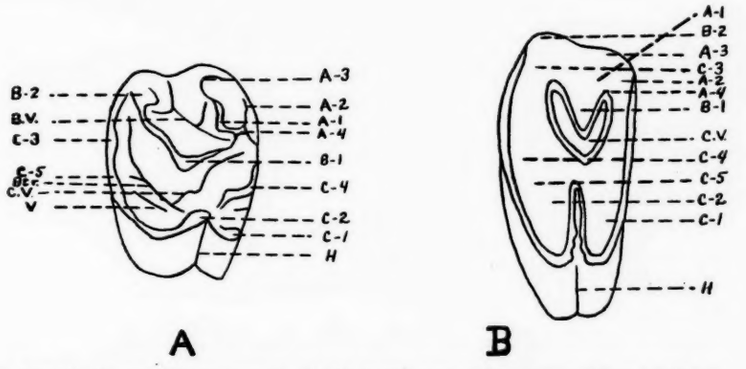



Fig. 115. Cusp terminology of lagomorph cheek teeth according to various authors.
(B = Burke, 1934; E = Ehik, 1925; T = usual application of tritubercular terminology by authors; W = terminology adopted in this paper.)

Fig. A, unworn P4; Fig. B, worn M1.

A–1. Part of metastyle and derivatives (W); part of metacone and associated styles (B); metacone in P3 (E); part of metastyle (T).
A–2. Part of metastyle and derivatives (W); part of metacone and associated styles (B); hypostyle (E); part of metastyle (T).
A–3. Part of metastyle and derivatives (W); part of metacone and associated styles (B); metastyle (E); part of metastyle (T).
A–4. Part of metastyle and derivatives (W); part of metacone and associated styles (B); part of metastyle (T).
B–1. Metacone (W); part of paracone (B); protocone (E); metacone (T).
B–2. Paracone (W); part of paracone (B); metacone except in P3 (E); parastyle (T).
C–1. Hypocone (W); hypocone (B); part of hypocone (E); hypocone (T).
C–2. Protocone (W); protocone (B); part of paracone (E); part of protocone (T).
C–3. Part of anteroloph (W); protoconule (B); part of parastyle (E); paracone (T).
C–4. Posterior crest (W); part of hypocone (E); metaconule (T).
C–5. Part of anteroloph (W); part of protoloph (B); part of parastyle (E); protoconule (T).
H. Hypostria (W); internal fold (B); internal reentrant (T).
B.V. Buccal valley (W).
Btr. Buttress (W); part of paracone (E).
C.V. Crescentic valley (W); lunate valley (B); crescent (T).
V. Unnamed valley (W); part of protocone (T).

studies of the occlusion, and assuming that the lower teeth are of normal pattern, as they seem to be, the second interpretation seems somewhat the most likely. With this interpretation, the metacone of *Palaeolagus* is greatly enlarged and the paracone reduced. Moreover, the latter has migrated buccad and become an appanage of the metacone. Another possible interpretation of the anterior part of the tooth is that the paracone is included in the anterior marginal crest, and the cusp above interpreted as the paracone is actually the mesostyle. This is more nearly in agreement with Ehik's interpretation (1926, Fig. 1).

Burke interprets the central lobe of P3, which seems homologous to the crescentic cusp of the buccal half of the molars, as the paracone, and the buccal lobe of P3, the equivalent of the postero-external cusp of the molars, as the metacone. Referring to the unworn P3 (Fig. 114J), the interpretation of the main buccal cusp as the mesostyle seems perhaps the more probable, but when dP2 is taken into consideration (Fig. 114E), this seems almost impossible. If the main buccal cusp is the metacone, and its antero-buccal appanage is the paracone, then the central lobe of P2 and dP2 would be the amphicone, which seems reasonable. The buccal lobe would then be an inflated metastyle, and the lingual lobe would be the protocone and hypocone. Altogether, this seems the most likely hypothesis of the cusp homologies, but until unworn teeth of Paleocene lagomorphs are found, this is about all that can be said, and any other hypothesis would be almost equally tenable. This interpretation differs considerably from those suggested by Burke (1934) and by Ehik (1926). In defense of Ehik's interpretations, it must be pointed out that he appears to have been the first author clearly to demonstrate the interdental homologies in the lagomorphs, and that no possible scheme of homology with the cusps of other mammals has come to light as yet which appears to satisfy the actual conditions. Burke reached essentially identical conclusions as to the premolar-molar development, but applied a different set of names to the cusps. It does not seem at all likely that in the leporid premolars there are cusps homologous to paracone, protocone and metacone, arranged in a transverse series, with the paracone internal and the metacone external, as Ehik postulated. Neither does it seem reasonable to assume that these three cusps are protocone, paracone and metacone, as Burke suggested, unless we assume very long pre-Uinta degeneration, which may well have occurred. Possibly the most logical interpretation of these cusps would be as the protocone, amphicone and metastyle, respectively. If this should be correct, all of the leporid upper cheek teeth would retain an undivided amphicone, the metastyle would remain persistently small, and the main development of the teeth would be through the hypertrophy of the protocone, its subsequent division into protocone and hypocone, and the growth of a crest along the anterior side of each tooth, arising from the protocone, and growing to the buccal side of the tooth, where it eventually unites with the mesostyle.

In view of the long pre-Uinta evolution through which the lagomorphs must have passed, it is quite possible that the ontogeny of the premolars has been foreshortened, and that they pass into the molariform stage in the quickest manner possible, which may or may not agree with the actual method by which the molars evolved into the same pattern. If this should prove to be the case, the application of premolar analogy to the molar pattern of the lagomorphs would lead to many errors, and the only safe manner in which to interpret the premolar pattern would be to wait until the discovery of a sufficient number of pre-Uinta lagomorphs to clarify the situation. It is quite possible that Forsyth-Major was correct when he considered the pattern of the anterior premolars as being due to reduction from a more molariform stage (1899, p. 453).

It might normally be expected that the premolar and milk molar series, if arranged from anterior to posterior, would represent an ascending evolutionary sequence, and that the molariform premolars would hold the key to the pattern of the true molars. Such sequences have, of course, been worked out from many groups of mammals. In some cases, however, premolar analogy cannot be applied, because the molars had already

attained their full pattern while the premolars were still undifferentiated, and when the mechanical forces of mastication brought about the convergence of the premolars to the molar pattern, the teeth developed in whatever manner the genes and the mechanics of tooth function permitted at the time, which might be entirely different in its details from that followed by the molars, though leading to a similar pattern in the end. Such a change would be analogous to the repairing of a machine which was performing an essential function and could not be stopped. The repairs must permit the constant functioning of the entire machine and yet bring the changed parts into harmony with the rest of the machine as quickly as possible. This would seem to me to be the most likely explanation of what has taken place in the lagomorphs. The molars attained a pattern, very similar to that of *Palaeolagus*, at an early date, perhaps in the Cretaceous or early Paleocene. The development of the lagomorph incisors, glenoid region and type of mastication proceeded *pari passu* with the molar evolution, and the two evolved in a harmonious whole as the parts of a single mechanism. According to this suggestion, the premolars at this time were relatively simple, having perhaps a single main cusp with an external and an internal cingulum, or perhaps a pattern entirely different. It is also possible that at this stage the completely gliriform nature of the anterior teeth and the long diastema were not fully established. At any rate, if this hypothesis should prove to be correct, the next stage would be a relatively sudden change in premolar patterns, to bring them into accord with the molar pattern and to increase the surface available for grinding, as opposed to the prehensile and cutting function of the hypothetical ancestral premolars. If this sequence should have been followed, it would be almost certain that the stages through which the premolars passed in their molarization would bear little or no resemblance to the corresponding stages in the evolution of the molar pattern, and there would be no basis for assuming that the cusps of the premolars would actually be homologous to the apparently similar cusps of the molars. On the other hand, it should be emphasized that there is no evidence that the development proceeded by way of the stages outlined above, and there is no evidence that the premolar cusps are not absolutely homologous to those of the molars. For the sake of simplicity, and in the entire absence of any evidence one way or the other, it has been assumed in the present work that the cusps of the premolars are actually homologous to those with which they appear to be homologous, but that they may not have passed through the same stages in reaching this ultimate pattern.

The lower teeth are sharply divided into two lobes, apparently representing the trigonid and the talonid. Except for the peculiarities of the upper teeth, there would be no reason for doubting this homology. The trigonid seems to consist of two main cusps, apparently the protoconid and the metaconid, and the talonid of two main cusps with a subsidiary one in the middle of the posterior side, apparently the hypoconid, entoconid and hypoconulid, respectively. One would not expect this pattern to have developed in the lower teeth without an approximately normal pattern developing in the upper molars. In $P\bar{3}$, there is a large anterior cusp, which may represent either a retained paraconid, or a neomorph, similar to the rodent anteroconid. No such cusp appears to be present on the other lower teeth, which supports the latter suggestion, although there is an anterior marginal crest on the trigonid in all teeth. If the anterior cusp of $P\bar{3}$ should turn out to be the paraconid, it would be a striking difference from the earlier rodents, and would suggest one point quite forcibly—that the rabbits lost their anterior premolars, i.e., became

gnawers, before the modifications of the upper teeth which entailed the loss of the paraconid in the lowers, thus allowing the retention of that cusp in $P\overline{3}$, whereas the rodents lost their anterior cheek teeth after these modifications had taken place. Indeed, the rodents that possess a cusp most nearly resembling a paraconid in location and relationships are those with but three cheek teeth, apparently the molars. If the above interpretations should be correct, it would demonstrate conclusively that the rodents and lagomorphs have been distinct groups at least as long as they have been gnawers, which means at least since they branched off from the central insectivore stock. The pattern of the upper molars of the lagomorphs, if correctly interpreted above, would demonstrate the same point, and strongly suggest that they have been an independent line since the Cretaceous.

There are two additional points about lagomorph cheek teeth which are worthy of further discussion. The deposition of cement has been discussed above in several places, but it might well be summarized here. When the tips of the cusps of a tooth of a member of one of the Oligocene genera are still below the level of the alveolus, there appears never to be any cement on the crown. Moreover, cement never appears on the intra-alveolar portion of an erupted tooth. This strongly suggests, if it does not prove, that the cement is deposited after the crown has passed above the level of the alveolus, and that the deposition is carried on by tissues lying above the alveolar level. Since the cement is deposited before the actual eruption of the tooth through the gums, this determines the time and locus of cement deposition with considerable accuracy. Of course, the deposition is a continuing process, a coating of cement being laid down on all portions of the continually erupting tooth as they pass through the zone of deposition.

The second point, the cessation of formation of the enamel, can be more clearly pictured from the lower teeth than from the uppers, though it occurs equally in both sets. After

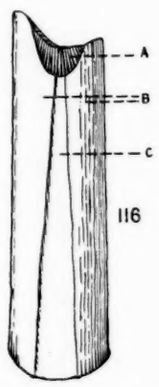



Fig. 116. *Palaeolagus intermedius*. M2 left. View of anterior side. A = surface worn by contact with $M\overline{1}$. B = enamel. C = dentine. × 5.

wear has proceeded until the hypoconulid has disappeared, the tooth attains an outline which it keeps for most of the animal's lifetime. After a very short additional time, however, the enamel ceases to be deposited on the anterior side of the tooth. If a tooth in this stage should be removed from the jaw, and viewed from the anterior side (Fig. 116),

the enamel will be seen to cover the entire face of the tooth near the wear surface, but to cover only the buccal and lingual sides near the pulp cavity. There is a long, slender isosceles triangle of dentine here, with no enamel cover. Since this part of the tooth is well down in the alveolus, inter-dental abrasion (H. E. Wood, 1938) could not have brought about this reduction in the enamel. It does not seem at all likely that abrasion between the tooth and the alveolus could account for this, nor that chemical resorption would have taken place. The only possibility remaining is that the roots have begun to form on the anterior side of the tooth, bringing about the cessation of enamel deposition, before they started to form on the rest of the tooth. This is a slight modification of the "unilateral hypsodonty" that has been described by Burke and Wilson as existing in the upper cheek teeth.

Although relationship has been suggested at one time or another between the lagomorphs and various other groups, nothing definite is known on the subject at the present time. The question of their ultimate relationships is entirely buried in Eocene or earlier deposits, and but little hope can be held out for a solution of the problem until the discovery of Lower Eocene lagomorphs, or, if *Eurymylus* should prove to belong to the order, until after the discovery of good material in a Paleocene horizon, or even earlier. The only pre-Uinta form that appears even remotely like the lagomorphs is *Eurymylus*, but this form throws no light on the broader relationships of the order, since it stands very far from all other known Paleocene mammals. In fact, if *Eurymylus* is not related to the lagomorphs, its relationships can not even be guessed at.

Certain similarities to Artiodactyls have been pointed out from time to time. Hürzeler (1936) is the most recent to raise this point, in his monograph on the caenotheres. As stated above elsewhere, he presents a detailed comparison of the tooth patterns of lagomorphs and caenotheres. Unfortunately, he compares worn lagomorph with unworn caenothere teeth, and has missed the detailed pattern of the former, which is quite different from that of the caenotheres. He points out certain other similarities in the skull and skeleton, but decides that most of these occur in several other groups, or are due merely to the similar size of the two forms, and reaches the conclusion that the parallel pattern of the molars is the only real similarity between the two groups. Since there is no fundamental resemblance of tooth pattern, this must also be ruled out as an indication of relationship. The skulls of *Caenotherium* and *Palaeolagus* are extremely different, the former being a typical artiodactyl and the latter a typical lagomorph in this respect. The slender snout, complete postorbital bars, large temporal fossa with well marked sagittal crest, and the high, narrow occiput of *Caenotherium*, are all in marked contrast with everything seen in *Palaeolagus*. The glenoid is in a normal position in the former, the anterior palatine fenestrae are small, and there is no reduction of the palate. And, of course, there is no enlargement of the incisors or tendency for the formation of a diastema in *Caenotherium*. This, however, would not necessarily be expected if the two forms were distantly related. Superficially, the vertebral column shows a number of similarities between the two groups, but these are more marked when *Caenotherium* is compared with *Lepus* than when it is compared with *Palaeolagus*, and closer study shows them mostly to be merely correlated with the similar size of the members of the two groups. If the lagomorphs are related to the caenotheres, I do not see how they could be more closely related than merely being members of the great ungulate stock. That is, there can be no specific relationship of

lagomorphs to caenotheres, though there may be a relationship between the lagomorphs and the artiodactyls.

The pattern of the upper cheek teeth of *Palaeolagus* is fundamentally different from that found among the rodents generally believed to be the most primitive members of the order, such as the Lower Eocene Paramyidae and the Bridger Sciuravidae and Ischyromyidae (see Part II of this volume, Figs. 8, 13 and 15 and Wilson, 1938, pp. 125–126 and various figures). In these rodents, there is an obvious tendency for the subdivision of the crown into protoloph and metaloph, with or without well developed conules. Among the rodents in general, the development of transverse crests has been the almost universal direction of dental evolution, correlated with the antero-posterior motion of the lower jaw in mastication. The striking difference in the direction of movement of the lower jaw should indicate that the two orders must have been entirely distinct at least as long as they have been gnawers.

An interesting parallel to the tooth pattern of the lagomorphs is that of *Coryphodon* (compare the figures in this paper with H. E. Wood, 1923, Fig. 2). In both forms, there is a heavy crest running the entire width of the anterior side of the tooth, curving posteriorly along the lingual side of the crown. In both, what appear probably to be the paracone and metacone form another crest, essentially paralleling the first, with the paracone at the buccal end and the metacone at the lingual end of this crest. In the lower teeth, the two groups are both much more normal in pattern than in the uppers. It is not desired to suggest that these resemblances between the lagomorphs and the coryphodonts are indicative of close relationship, but it does seem possible that this might be an indication, in a general way, of the primary mammalian group to which the lagomorphs may belong, since it is well known that parallelism is much more common and perfect among related than unrelated forms.

The only animal that appears to show a close fundamental resemblance to the lagomorphs, that I know of, is *Eurymylus*. Matthew and Granger (1929, p. 7) pointed out this resemblance, though they stressed its resemblances to certain of the more specialized rodents, a resemblance which has always appeared rather far-fetched to the present author. A careful study of the teeth of all the available specimens of *Eurymylus* emphasizes this difference in pattern, and also increases the points of similarity to the lagomorphs. The fragments of the skull and mandible associated with the teeth are also rather like those of lagomorphs. The present is not a fitting place to enter into a discussion of these similarities, but I believe that almost every feature of *Eurymylus* can be matched in the lagomorphs and not in any other group of any order. *Eurymylus*, however, is so entirely isolated that its inclusion among the lagomorphs would not settle any of the fundamental problems of relationship of either group. It would merely emphasize the length of time that the lagomorphs have been a distinct stock, since the Gashato would appear probably to be Upper Paleocene.

Since Gidley raised the lagomorphs to ordinal status, the suggestion has occasionally been made that the lagomorphs and rodents, while distinct orders, may be members of a superorder for which Linnaeus' term "Glires" could well be revived. At the present time, my feeling on this matter is that if the relationship of the two orders should ever be established, such a superordinal union would be an excellent description of the facts. However, I know of no characters found in both the rodents and the lagomorphs that do

not appear either to be similar adaptations to a similar habitus, due to parallelism in general, or primitive characters that have been retained since both orders have specialized on a low plane of development. Therefore, it appears unjustifiable to attempt to unite the two orders under the term Glires, at the present time.

In summary, the only conclusion that I would feel sure of, for the time being, is that whatever their ultimate relationships, the lagomorphs are a very ancient mammalian stock, presumably Eutherian, which has evolved, at a slow rate, as an entirely independent line at least since the Paleocene and perhaps since the Mesozoic. There appears never to have been any great radiation of the group, but rather always to have been several closely allied lines, all conservative. At any one time, one or more of these lines may be very successful as a group, and its members may be one of, if not the, most abundant groups in the fauna, and there may be a considerable number of species and subspecies, as at the present time, but this individual success has never led either to an increase in the tempo of lagomorph evolution or to any great divergence, either from one another or from the ancestral stock, of the forms included in the order. This suggests as one alternative that the lagomorphs early became well adapted for a particular ecologic niche, and that the passing of subsequent eras has brought but little change in that niche, and hence but little change in the lagomorphs. Another possibility is that this order is a generalized stock, fitted for any of a number of ecologic niches; that one or another of these environments is present almost universally for most of the time, and continuously in many places; and that for some reason the lagomorphs are a very stable group, genetically, so that mutations of a specializing type take place relatively rarely.

DISTRIBUTION OF WHITE RIVER LAGOMORPHA

| | *Pipestone Springs* | *Three Forks* | *Cypress Hills* | *Chadron* | *Oreodon Beds* | *Cedar Creek* | *Leptauchenia Beds* |
|---|---|---|---|---|---|---|---|
| *Megalagus brachyodon* | X | | 1 | 2 | | | |
| *Megalagus turgidus* | | | 1 | 2 | X | X | ? |
| *Desmatolagus dicei* | X | | | | | | |
| *Desmatolagus gazini* | | | | | X | | |
| *Palaeolagus temnodon* | X | X | X | 3 | | | |
| *Palaeolagus haydeni* | | | | 3 | X | X | X |
| *Palaeolagus intermedius* | | | | | 4 | X | |
| *Palaeolagus burkei* | | | | | ? | | X |

1. Cope (1885, 1889 and 1891) and Lambe (1908) mention *Palaeolagus turgidus* from these beds. The material is very likely *Megalagus brachyodon.*
2. Cook and Cook (1933) mention *Palaeolagus turgidus* from these beds. The material is very likely *M. brachyodon.*
3. Cook and Cook (1933) mention *Palaeolagus haydeni* from these beds. The material is very likely *Palaeolagus temnodon.*
4. Fide Cook and Cook (1933).

In the White River, there were three distinct groups of lagomorphs, represented by the three genera discussed above. Of these, *Palaeolagus* was the most progressive in dental characters, though perhaps more primitive in the skeleton. It probably is close to the ancestral line of the later leporids, if it is not the actual ancestor. There is no evidence that the *Megalagus* and *Desmatolagus* stocks persisted after the Lower Miocene. However, the complete reluctance on the part of most authors to study the lagomorphs has led to an entire blank in the published record of the order throughout most of the Miocene, and an almost equally blank record in the Pliocene, except for the work that has been done on the Pacific coast and the worthless reference of specimens to "*Lepus* sp.". For this reason, the *Megalagus* and *Desmatolagus* lines may have persisted much longer than now appears to be the case, and there may easily have been other lines that are still entirely unknown. When the lagomorphs from the Great Plains Miocene and Pliocene are more thoroughly studied, it will be much easier to work out the lagomorph phylogeny. For the present, it can only be said that *Palaeolagus* seems closest to *Archaeolagus*, and that *Megalagus* and *Desmatolagus* appear to be aberrant lines. *Mytonolagus* belongs to the *Megalagus* phylum, so that nothing is known of the ancestry of *Palaeolagus*. There is no evidence of North American ochotonids until the later Tertiary. Nothing can be stated concerning the origin of the Leporinae except that they were not descended from *Hypolagus*. The accompanying chart shows the distribution of the White River Lagomorpha.

## REFERENCES


Burke, J. J. 1934. Mytonolagus, a new leporine genus from the Uinta Eocene series in Utah. Annals Carnegie Mus., XXIII, pp. 399–420, 1 pl.

1936. Ardynomys and Desmatolagus in the North American Oligocene. Annals Carnegie Mus., XXV, pp. 135–154, 7 figs.

Camp, Charles L., and A. E. Borell. 1937. Skeletal and muscular differences in the hind limbs of Lepus, Sylvilagus and Ochotona. Journ. Mammalogy, XVIII, no. 3, pp. 315–326, 6 figs.

Cook, Harold J., and M. C. Cook. 1933. Faunal lists of the Tertiary vertebrata of Nebraska and adjacent areas. Nebr. Geol. Surv., Paper No. 5, 58 pp.

Cope, E. D. 1873*a*. Second notice of extinct Vertebrata from the Tertiary of the Plains. Paleontological Bull. No. 15, pp. 1–6.

1873*b*. Synopsis of new Vertebrata from the Tertiary of Colorado, obtained during the summer of 1873. Washington, Gov't Printing Office, pp. 1–19.

1873*c*. Third notice of extinct vertebrata from the Tertiary of the Plains. Paleontological Bull. No. 16, pp. 1–8.

1884. The Vertebrata of the Tertiary formations of the West. Rept. U. S. Geol. Surv. Terr., III, pp. i–xxxv, 1–1009, Pls. I–LXXV*a*.

1885. The White River Beds of Swift Current River, Northwest Territory. Amer. Nat., XIX, p. 163.

1889. The vertebrata of the Swift Current River. II. Amer. Nat., XXIII, pp. 151–155.

1891. On vertebrata from the Tertiary and Cretaceous rocks of the Northwest Territory. I. The species from the Oligocene or Lower Miocene beds of the Cypress Hills. Geol. Surv. Can., Contr. to Can. Palaeont., III, pp. i, 1–25, Pls. I–XIV.

Davis, William B. 1936. Young of the Brush Rabbit, Sylvilagus bachmani. The Murrelet, XVII, pp. 36–40, 4 figs.

Dice, L. R. 1917. Systematic position of several American Tertiary lagomorphs. Univ. Cal. Publ., Bull. Dept. Geol., X, No. 12, pp. 179–183, 6 figs.

1929. The phylogeny of the Leporidae, with description of a new genus. Jour. Mammalogy, X, no. 4, pp. 340–344.

1932. Notes on *Hypolagus browni* and *Lepus benjamini*, fossil hares from the Pleistocene of Arizona. Papers Michigan Acad. Sci., Arts and Letters, XVI, pp. 379–382, 3 figs.

1933. Some characters of the skull and skeleton of the fossil hare, *Palaeolagus haydeni*. Papers Michigan Acad. Sci., Arts and Letters, XVIII, pp. 301–305, 2 pls.

AND D. S. DICE. 1935. The lower cheek teeth of the fossil hare *Palaeolagus haydeni*. Papers Michigan Acad. Sci., Arts and Letters, XX, pp. 455–463, Figs. 7–25, Pl. XCIII.

DOUGLASS, E. 1901. Fossil mammalia of the White River Beds of Montana. Trans. Amer. Phil. Soc., XX, pp. 237–279, Pl. IX.

EHIK, J. 1926. The right interpretation of the cheekteeth tubercles of Titanomys. Annales Musei Nationalis Hungarici, XXIII, pp. 178–186, 5 figs.

GAZIN, C. L. 1934. Fossil hares from the late Pliocene of southern Idaho. Proc. U. S. Nat. Mus., LXXXIII, No. 2976, pp. 111–121, 5 figs.

GIDLEY, J. W. 1912. The lagomorphs an independent order. Science, n.s., XXXVI, No. 922, pp. 285–286.

HALL, E. R. 1930. Rodents and lagomorphs from the Later Tertiary of Fish Lake Valley, Nevada. Univ. Cal. Publ., Bull. Dept. Geol. Sci., XIX, No. 12, pp. 295–312, Pl. XXXVII, 29 figs.

HÜRZELER, J. 1935. Osteologie und Odontologie der Caenotheriden. Abh. Schweiz. Palaeont. Gesellschaft, LVIII–LIX, pp. 1–109, 8 pls., 72 figs.

KORMOS, T. 1934. Zur Frage der Abstammung eurasiaticher Hasen. Allat. Közlem., XXXI, pp. 65–78, 3 figs.

LAMBE, L. M. 1908. The vertebrata of the Oligocene of the Cypress Hills, Saskatchewan. Geol. Surv. Can., Contr. to Can. Palaeont., III, Pt. 4, 65 pp.

LEIDY, J. 1856. Notices of remains of extinct Mammalia, discovered by Dr. F. V. Hayden in Nebraska Territory. Proc. Acad. Nat. Sci. Phila., VIII, pp. 88–90.

MAJOR, C. J. F. 1899. On fossil and recent Lagomorpha. Trans. Linn. Soc. London, series 2, VII, pp. 433–520, Pls. XXXVI–XXXIX.

MATTHEW, W. D. 1899. A provisional classification of the fresh-water Tertiary of the West. Bull. Amer. Mus. Nat. Hist., XII, pp. 19–75.

1901. Fossil mammals of the Tertiary of Northeastern Colorado. Mem. Amer. Mus. Nat. Hist., I, Pt. 7, pp. 353–447, Pls. XXXVII–XXXIX, 34 figs.

1902. A horned rodent from the Colorado Miocene. With a revision of the Mylagauli, Beavers and Hares of the American Tertiary. Bull. Amer. Mus. Nat. Hist., XVI, Art. 22, pp. 291–310, 17 figs.

1903. Fauna of the Titanotherium Beds at Pipestone Springs, Montana. Bull. Amer. Mus. Nat. Hist., XIX, Art. 6, pp. 197–226, 19 figs.

1915. Climate and Evolution. N. Y. Acad. Sci., Annals, XXIV, pp. 171–318.

AND W. GRANGER. 1923. Nine new rodents from the Oligocene of Mongolia. Amer. Mus. Novitates No. 102, 10 pp., 12 figs.

W. GRANGER AND G. G. SIMPSON. 1929. Additions to the fauna of the Gashato Formation of Mongolia. Amer. Mus. Novitates No. 376, 12 pp., 13 figs.

RUSSELL, L. S. 1934. Revision of the Lower Oligocene Vertebrate Fauna of the Cypress Hills, Saskatchewan. Trans. Roy. Can. Inst., XX, pt. 1, pp. 49–67, 4 pls.

SCHLAIKJER, E. M. 1935. Contributions to the stratigraphy and paleontology of the Goshen Hole area, Wyoming. IV. New vertebrates and the stratigraphy of the Oligocene and early Miocene. Bull. Mus. Comp. Zool., LXXVI, No. 4, pp. 97–189, 41 pls., 13 figs.

SCHLOSSER, M. 1884. Die Nager des europäischen Tertiärs nebst Betrachtungen über die Organisation und die geschichtliche Entwicklung der Nager überhaupt. Palaeontographica, XXXI, 143 pp., 8 pls., 12 figs.

SCHREUDER, A. 1936. Hypolagus from the Tegelen Clay; with a note on recent Nesolagus. Arch. Néerland. Zool., II, pp. 225–239, 6 figs., 1 pl.

SIMPSON, G. G. 1933. A new classification of Mammals. Bull. Amer. Mus. Nat. Hist., LIX, 5, pp. 259–293.

TROXELL, E. L. 1921. Palaeolagus, an extinct Hare. Amer. Jour. Sci., series 5, I, 22, pp. 340–348, 20 figs.

TULLBERG. T. 1897. Über das System der Nagethiere. Eine Phylogenetische Studie. Mit. Köng. Gesel. Wissen., Upsala, pp. 1–514 + 18, Pls. I–LVII.

VIRET, J. 1929. Les faunes de mammifères de l'Oligocène Supérieur de la Limagne Bourbonnaise. Annales de l'Université de Lyon, n.s., Pt. I, XLVII, pp. 1–328, 31 pls., 32 figs.

WALKER, M. V. 1931*a*. Notes of fossil lagomorphs. Trans. Kansas Acad. Sci., XXXIV, pp. 122–124.

1931*b*. Notes on North American fossil lagomorphs. Aerend, II, No. 4, pp. 227–240, 1 fig.

WILSON, R. W. 1934. Two rodents and a lagomorph from the Sespe of the Las Posas Hills, California. Carnegie Inst. Wash. Publ. No. 453, Pt. 2, pp. 11–17, 1 fig., 1 pl.

1938. Review of some rodent genera from the Bridger Eocene. Part I. Amer. Jour. Sci., series 5, XXXV, pp. 123–137, 4 figs.

WOOD, A. E. 1937*a*. Additional material from the Tertiary of the Cuyama Basin of California. Amer. Jour. Sci., series 5, XXXIII, pp. 29–43, 21 figs.

1937*b*. The Mammalian Fauna of the White River Oligocene. Part II. Rodentia. Trans. Amer. Phil. Soc., n.s., XXVIII, part 2, pp. 155–269, Figs. 8–70, Pls. XXIII-XXXIII.

WOOD, H. E. 2ND. 1923. The problem of the Uintatherium molars. Bull. Amer. Mus. Nat. Hist., XLVIII, Art. 18, pp. 599–604, 4 figs.

1938. Causal factors in shortening tooth series with age. Jour. Dental Research, XVII, No. 1, pp. 1–13, 5 figs.

AND A. E. WOOD. 1937. Mid Tertiary vertebrates from the Texas coastal plain: fact and fable. Amer. Midland Naturalist, XVIII, No. 1, pp. 129–146, 4 figs., 1 pl.

WOOD-JONES, F. 1929. Some landmarks in the phylogeny of the primates. Human Biology, Vol. I, pp. 214–228.

# EXPLANATIONS OF PLATES XXXIV AND XXXV

PLATE XXXIV. This plate was inadvertently omitted from Part II of this volume.

*Ischyromys typus*, Amer. Mus. Nat. Hist. No. 12,247.

Fig. 1. Skull, left side.
Fig. 1*a*. Skull, top.
Both figures × 2.

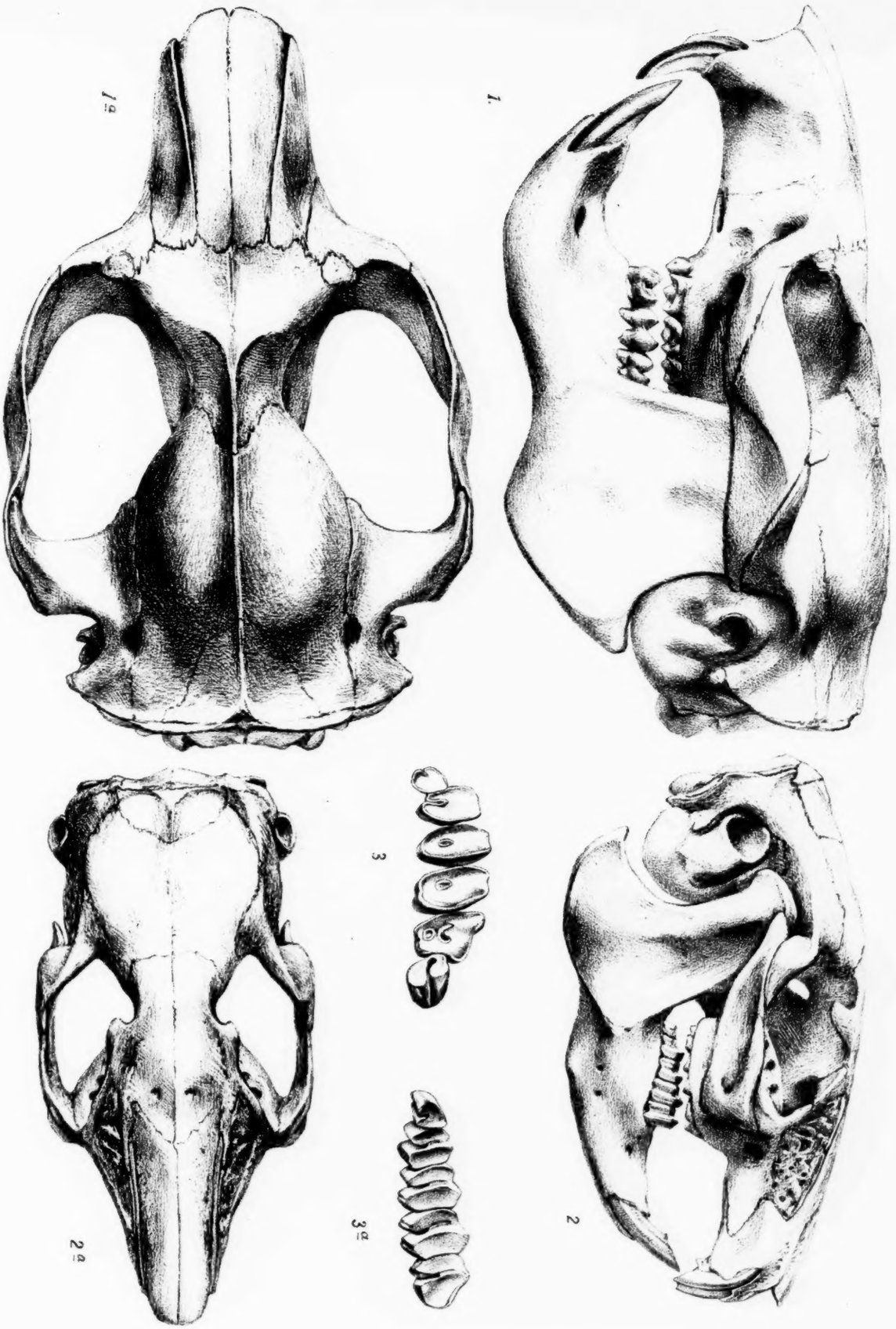
*Palaeolagus haydeni*, U. S. Nat. Mus. Nos. 10,356 and 13,611.

Fig. 1. Skull, right side.
Fig. 1*a*. Skull, top.
Fig. 2. Right upper cheek teeth.
Fig. 2*a*. Right lower cheek teeth.
Figs. 1 and 1*a* × 3, Figs. 2 and 2*a* × 6.

PLATE XXXV

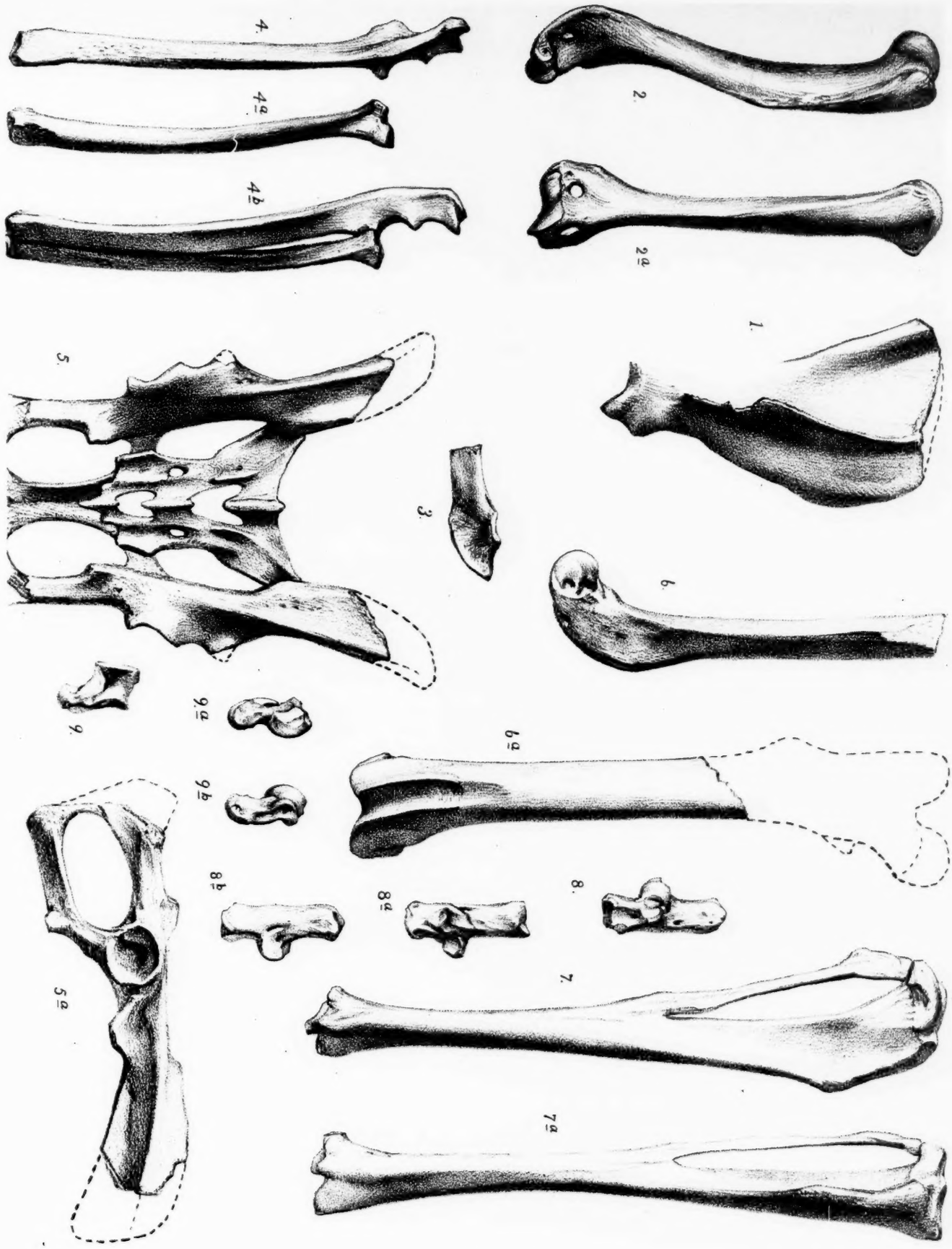
*Palaeolagus haydeni*, Univ. Michigan No. 14,317.

Fig. 1. Right scapula.
Fig. 2. Right humerus, external side.
Fig. 2*a*. Right humerus, front.
Fig. 3. Manubrium, side.
Fig. 4. Right ulna, rear.
Fig. 4*a*. Right radius, rear.
Fig. 4*b*. Right radius and ulna, side.
Fig. 5. Sacrum and pelvis, top.
Fig. 5*a*. Right pelvis.
Fig. 6. Right femur, side.
Fig. 6*a*. Right femur, front.
Fig. 7. Right tibio-fibula, side.
Fig. 7*a*. Right tibio-fibula, front.
Fig. 8. Right calcaneum, external side.
Fig. 8*a*. Right calcaneum, top.
Fig. 8*b*. Right calcaneum, internal side.
Fig. 9. Right astragalus, top.
Fig. 9*a*. Right astragalus, external side.
Fig. 9*b*. Right astragalus, internal side.




ISCHYROMYS—PALAEOLAGUS

FULL-TONE MERIDEN




PALAEOLAGUS

FULL-TONE MERIDEN

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# THE MAMMALIAN FAUNA OF THE WHITE RIVER OLIGOCENE

WILLIAM BERRYMAN SCOTT AND GLENN LOWELL JEPSEN

## PART III. LAGOMORPHA

ALBERT ELMER WOOD

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